INTERACTIONS OF PREDATORS, HABITAT AND CONSPECIFICS ON THE COASTAL DISTRIBUTION OF AGE 0 JUVENILE COD (Gadus SPP.) IN NEWFOUNDLAND

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by

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ABSTRACT

Newly settled age 0 juvenile cod, Atlantic cod *Gadus morhua* and Greenland cod *Gadus ogac*, coexist in nearshore areas around Newfoundland, but little is understood on the mechanisms affecting their distribution. In young marine fish, predation risk is often high yet there is generally an increasing capacity in larger individuals to evade predators. It is therefore difficult to distinguish the role of behaviour and differential survival on distribution of fish in their early life stages. In a series of field and laboratory experiments, I investigate how habitat complexity, predators and conspecific density interact to affect survival and behaviour in juvenile cod, and ultimately, their distribution in coastal Newfoundland.

In a bay-scale study (~10 km^2), I monitored patterns of settlement and distribution of *G. morhua* and *G. ogac*, following a large-scale alteration of nearshore eelgrass (*Zostera marina*) habitat. Comparisons of bi-weekly sampling between control and experimental sites from 1995-2001 indicated a significant increase in cod abundance at sites enhanced with simulated eelgrass and a corresponding decrease in cod numbers at sites where eelgrass had been removed. These data supported predictions, demonstrating that: 1) there was a sufficient supply of juvenile cod within the range of areas that have historically been unoccupied (i.e. sand) and 2) both species preferred to settle in complex habitats. However, *G. ogac* responded significantly to the removal of eelgrass in more comparisons than *G. morhua* (70% and 37% respectively), suggesting that *G. ogac* have a higher affinity for complex vegetative habitats than *G. morhua* at the scale of manipulation (*ca.* 800m^2). Furthermore, despite an overall preference for eelgrass habitat, high within-site catch variation indicated that individuals of both species were not

restricted to any single seine site. Rather, the highly variable data indicate that juvenile cod were mobile and occasionally aggregated throughout the study period. My results support previously described juvenile cod-eelgrass associations but contradict other published accounts of high site-attachment and restricted movement in *G. morhua* following settlement.

In a second study, fish density, movement and schooling behaviour were examined in *G. morhua* and *G. ogac* using a combination of field-seines, mark-recapture- and laboratory experiments. Density estimates from seines (n=427) over five years (1996, 1998-2001) indicated that these species associated with eelgrass but periodically were detected in high abundance over sand. Within-site catch variation indicated both species aggregated more in sand than eelgrass habitat, and in *G. morhua*, aggregations over sand increased as density in eelgrass increased. Although such patterns in catch data could be interpreted as the effects of differential mortality between habitats, a mark-recapture experiment indicated that both species of cod were not site-attached and moved between seine locations. Furthermore, video-analysis from laboratory experiments demonstrated that cod formed tighter aggregations over sand compared to eelgrass habitats. The results demonstrate that juvenile cod modify their behaviour with changing density, possibly as a means of exploiting poor quality habitats when high quality habitats are saturated with conspecifics. Consequently, habitat suitability for *G. morhua* should be considered a dynamic rather than fixed variable in density-dependent habitat models.

In a third study, I measured the effect of predator density and habitat patch size in age 0 juvenile cod in a nearshore field experiment. Eelgrass patch size was altered using artificial eelgrass mats of five sizes (0.32, 1.1, 5.5, 11 and 22 m^2) and subsequently

deployed in duplicate at each of two sites in Newman Sound in Terra Nova National Park during summer-autumn, 1999 and 2000. Predator distribution was determined using a combination of weekly underwater transect surveys and biweekly seining. Relative predation rates were measured by tethering age 0 cod at the center of each patch and recording the incidence of predation (n=1116 tether sets). Predation rates were negatively correlated with patch size during both years, suggesting that larger patches reduce predator foraging ability. However, high predator densities in the largest eelgrass patch resulted in higher than expected rates of predation. Therefore habitat dimension affected predation risk in juvenile cod via two opposing mechanisms. The results emphasize the importance of considering both habitat areal extent and predator distribution when estimating the effects of habitat fragmentation on predation rates.

In a final, small-scale study (<2 m^2), I examined the spatial conflict between age 0 juvenile cod and their predators, shorthorned sculpin (*Myoxocephalus scorpinus*) and age 3+ Atlantic cod, in complex and simple habitats. Predators and prey were videotaped using a novel method using light and shadow to determine fish position in three-dimensions. Results indicated that both habitat and predator type interacted to form unique patterns of space occupation by predators and prey. Spatial overlap between predators and prey was highest in open habitat in the presence of age 3+ cod (a cruising predator) but lowest in the presence of sculpin (an ambush predator) in the same habitat. In eelgrass, spatial conflicts between predators and prey were resolved along the vertical component; age 0 cod remained above eelgrass in the presence of sculpin but used the structure in the presence of an age 3+ cod predator. Anti-predator behaviour (i.e., predator-prey distance, prey cohesion, angle separation and "freezing") was significantly

reduced over eelgrass compared to sand, suggesting eelgrass has lower 'inherent risk' than open habitats. However, predation mortality was similar across all treatments. This raises the question why age 0 cod relax their anti-predator behaviour in complex habitats. I suggest that complex habitats also impair the visual cues needed to perform anti-predator behaviour (e.g., schooling) and locate predators. Alternatively, the reduced anti-predator behaviour in complex habitats may reflect the fitness costs (i.e., lost foraging opportunities) of using these behaviours in all environments.

I conclude from these studies that behaviour, ranging in scales from $< 1m^2$ to $> 1000m^2$, plays an important role in shaping distributions of age 0 juvenile cod in the nearshore. Behavioural decisions were largely made in response to the predation risk associated with predator distribution and refuge characteristics of habitat. Therefore, nearshore distributions of age 0 juvenile cod are not simply the result of differential mortality between areas of higher and lower risk. Consequently, these results provide information on home range, habitat preference and aggregation behaviour that would be relevant to future efforts in the conservation of Atlantic cod.

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I would like to take this space to thank the additional people not listed at the end of each chapter. These include my supervisor, Joe Brown, for all his support and good-natured philosophy, Bob Gregory, for his invaluable contribution in the field and comments on manuscripts and lastly, David Schneider, for his critical comments on statistical analyses and manuscripts. Lastly, I would like to thank my wife, Louise, my parents, Jim and Sharon, and my family in Newfoundland, Doug and Margaret, for their support, encouragement and general goodwill while producing this thesis.

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Chapter 1:

General Introduction

The interactions of fish with predators and habitat are considered to be fundamental determinants of fish distribution. These interactions can be magnified during early life stages when predator vulnerability is highest and refuge habitat is most critical (e.g., Sogard 1997). A firm understanding of interactions between juvenile fish, their predators and available habitat therefore has an important bearing on species management, exploitation and conservation.

In the following chapters, I examine the role of predators and habitat on juvenile Atlantic cod (*Gadus morhua*) behaviour and distribution, an important commercial and ecological species residing off the coast of Newfoundland. Unlike other habitat studies with juvenile Atlantic cod (e.g., Lough et al.1989, Keats 1990, Gotceitas and Brown 1993, Methven and Badjik 1994, Tupper and Boutilier 1995ab, Grant and Brown 1998ab, Lindholm 1999), I use an experimental approach over a range of scales while also considering changes in predator behaviour and distribution. Through an experimental approach I hope to resolve some of the discrepancies in habitat use reported in other studies (e.g., Tupper and Boutilier 1995ab and Gotceitas et al. 1997) and reveal the mechanisms of variable habitat use in this species. I explore these mechanisms at a range of scales from 1×10^{-3} m^2 to 1×10^{6} m^2 as the survival and growth associated with a particular habitat at one scale may be irrelevant at another (e.g., larval supply, Jenkins et al. 1998). I also compare Atlantic cod with Greenland cod *Gadus ogac* to probe basic life-history influences on behaviour and distribution patterns. I do this in four related studies.

In Chapter 2, I examine variable habitat use at large scales. Previous studies in Newfoundland suggest eelgrass is preferred habitat based on small-scale lab studies (e.g., Gotceitas et al. 1997, but there is no evidence juvenile cod select habitat at scales greater than $4m^2$. I examine large-scale habitat selection in age 0 *G. morhua* and *G. ogac* by removing and adding large sections of eelgrass along nearshore areas of Bonavista bay, Newfoundland. I then compare the variable habitat use of habitat by juvenile cod both before and after the manipulation over six years of sampling (3 yrs pre-, 3 years post). My *in situ* experimental approach decouples eelgrass from other environmental variables (i.e., freshwater inlet, enriched substrate, larval supply), and consequently, I am able to determine if eelgrass is responsible for observed settlement and post-settlement distribution.

In Chapter 3, I explore the importance of density-dependence on changes in behaviour and ultimately, distribution of age 0 juvenile cod. In Chapter 3, I also explicitly measure the mechanisms of variable habitat use that were observed and discussed in Chapter 2. I do this by examining a long-term data set (6yrs) of juvenile cod distribution, a mark-recapture study and behavioural observations in the laboratory. Specifically, I examine whether large-scale patterns in habitat use are the result of behaviour (i.e., movement and aggregation) or differential mortality. I further discuss the importance of considering behavioural flexibility in the context of density-dependent models.

In Chapter 4, I focus my examination of juvenile cod-habitat interactions to intermediate scales ($0.3\ m^2$ to $22m^2$). In Chapter 2, I demonstrated that cod prefer eelgrass over unvegetated habitat at large scales ($880m^2$), but it should be expected that

refuge benefits decrease as habitat size decreases as the result of edge effect enhanced predation. I examine these mechanisms *in situ* by measuring consumption rates of juvenile cod tethered to varying patch sizes of eelgrass over two experimental years. I analyze changes in predation rate as a function of patch size and as a function of localized predator distribution. Aquatic studies examining edge effects are rare, and fewer studies (terrestrial or aquatic) simultaneously examine variable predator density when measuring predation rates. Therefore the experiment is novel both in juvenile cod ecology and ecological theory.

Finally, in Chapter 5, I narrow my examination of juvenile cod-predator-habitat relationships further to scales $<3m^2$. Observations from the preceding chapters indicate that predators and prey coexist in eelgrass and unvegetated sand, but it remains unclear how predator-prey behaviour is resolved at small scales. In chapter 5, I simultaneously examine the behaviour of juvenile cod and their predators over eelgrass and unvegetated sand using video and image analysis. Here, I also introduce a novel method of measuring fish position in three-dimensions using a single camera and multiple light sources.

In my conclusion, I summarize the results of my work and discuss the implications of juvenile cod behaviour and habitat association on fisheries management, survey design and conservation measures.

For each chapter, I played major role in conceiving, executing, analyzing and writing of each chapter. However, I would like to also acknowledge the contributions by others that merit authorship in this thesis. They are Dr. Robert Gregory (Chapters 2, 3, 4 and 5) , Dr. Joe Brown (Chapters 2, 3, 4 and 5), Dr. David Schneider (Chapter 3), Chris Laurel (Chapter 5) and Janelle Hancock (Chapter 3).

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CHAPTER 2:

Settlement and distribution of age 0 juvenile cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation.

ABSTRACT:

Understanding the mechanisms leading to variable habitat use by fish is of fundamental importance to both ecologists and fisheries managers. In Bonavista Bay, Newfoundland, I monitored patterns of settlement and distribution of two species of gadids, Atlantic cod (*Gadus morhua*) and Greenland cod (*G. ogac*), following a large-scale alteration of nearshore eelgrass (*Zostera marina*) habitat. Comparisons of bi-weekly sampling between control and experimental sites from 1995-2001 indicated a significant increase in cod abundance at sites enhanced with simulated eelgrass and a corresponding decrease in cod numbers at sites where eelgrass had been removed. These data supported predictions, demonstrating that: 1) there was a sufficient supply of juvenile cod within the range of areas that have historically been unoccupied (i.e. sand) and 2) both species preferred to settle in complex habitats. However, *G. ogac* responded significantly to the removal of eelgrass in more comparisons than *G. morhua* (70% and 37% respectively), suggesting that *G. ogac* have a higher affinity for complex vegetative habitats than *G. morhua* at the scale of manipulation (*ca.* 800m^2). Furthermore, despite an overall preference for eelgrass habitat, high within-site catch variation indicated that individuals of both species were not restricted to a single seine site. Rather, the highly variable data indicate that juvenile cod were mobile and occasionally aggregated throughout the study

period. My results support previously described juvenile cod-eelgrass associations but contradict other published accounts of high site-attachment and restricted movement in *G. morhua* following settlement.

KEY WORDS: Eelgrass · Habitat selection · Atlantic cod · Greenland cod · Habitat enhancement · Unvegetated sand

INTRODUCTION:

The identification of critical nursery habitat has become an important task for the management of commercially important fish species (e.g. Schmitten 1996). Although habitat use is known to be species-specific, many studies have demonstrated that nearshore abundance and diversity of juvenile fish is often higher in eelgrass (*Zostera* spp.) habitats relative to simple, unvegetated mineral substrates (Bell and Pollard 1989, Edgar and Shaw 1995, Mattila et al. 1999). Eelgrass has been shown to provide refuge to juvenile fish species in laboratory observations (Gotceitas et al. 1995, Gotceitas et al. 1997), tethering studies (Linehan et al. 2001, Laurel et al. 2003) and predator exclusion experiments (Hindell et al. 2000). High food levels (Connolly 1994, Parker et al.2001), reduced physical exposure (Bell and Pollard 1989) and increased water quality (Orth 1984) are other possible benefits of nearshore eelgrass habitat to juvenile fish.

Regardless of the survival and growth benefits associated with eelgrass, habitat quality may not always predict fish distribution. Competitive interactions may prevent pelagic juveniles from initially settling in areas of preferred habitat (Sweatman 1985). Post-settlement processes (e.g. emigration or mortality) may later reshape distributions of juvenile fish settling in poor quality habitat (e.g. Tupper & Boutilier 1995a). Fish-habitat relationships can also break down due to large-scale processes such as differential larval supply (Bell & Westoby 1986, Caselle & Warner 1996, Jenkins et al.1997a, Jenkins et al. 1998). Jenkins et al. (1996) found that juvenile whiting abundance decreased in eelgrass habitats further from the spawning ground, a result attributed to a diminishing supply of pre-settling juveniles. Differential larval supply may also affect overall community

structure in eelgrass, including the abundance and diversity of juvenile fish and their prey species (Bell et al. 1988). Although these patterns may disappear through eventual movement to a habitat of higher quality (Sogard 1987), initial settlement patterns have prolonged effects on the distribution of fish if post-settlement movement is limited (Bell & Westoby 1986, Tupper & Boutilier 1995a). Therefore, evaluating critical nursery habitat for juvenile fish has to be considered from multiple spatial and temporal scales.

Generally, habitat studies have been conducted as either small-scale experiments or as large-scale field observations. Small-scale experiments are typically performed in the laboratory to investigate behaviour of an organism when selecting habitat. In such experiments, habitat selection is typically determined by giving a fish a choice between two or more habitats of equal area. Predators or food may be introduced to determine how fish choose habitats when faced with trade-offs between predator risk and opportunities for faster growth (Werner et al. 1983, Schmitt & Holbrook 1985, Holbrook & Schmitt 1988). Laboratory studies are useful in isolating small-scale processes, but may not always reflect patterns of habitat use at large scales. Alternatively, large-scale field studies are unable to determine mechanisms of habitat use. Although juvenile fish distribution can be correlated with large-scale phenomena (e.g. physical processes, pelagic larval supply, predator distribution, etc), causality is difficult to determine without controlled experiments. Consequently, it is difficult to resolve the contribution of small (e.g., behavioural) and large (e.g., oceanographic) scale processes to habitat use patterns in fish.

One solution is to conduct controlled *in situ* experiments with habitat at large scales. Aquatic field experiments are not novel, but seagrass manipulations are typically

restricted to less than 4 m^2 (Sogard 1989; Irlandi 1997; Horinouchi & Sano 1999; Lee et al.2001; Jenkins et al.2002). Larger-scale habitat manipulations are ideal when investigating fish-habitat relationships, but spatial replication of these studies is logistically difficult. Similarly, removing large areas of potentially critical fish habitat may have long-term detrimental consequences to the species being investigated. However, recent statistical tools using randomized time replicates in conjunction with historical data have reduced statistical requirements for spatial replication (Randomized Intervention Analysis – RIA, Carpenter et al.1989). With such tools, it is logistically possible to carry out large-scale habitat manipulation experiments.

We conducted a large-scale habitat manipulation experiment to determine the effect of eelgrass (*Zostera marina*) on the distribution of juveniles of two cod species, Atlantic cod (*Gadus morhua*) and Greenland cod (*G. ogac*). Age 0 juvenile cod associate with a number of high-structured demersal habitats (i.e. reefs, cobble, eelgrass; Lough et al. 1989, Tupper & Boutilier 1995ab). However, juvenile cod distribution in the waters off Newfoundland is almost exclusively restricted to eelgrass habitat in nearshore areas (Gotceitas et al.1997), where abundance is highly variable among beds of this plant (Grant & Brown 1998a). In this study, I added and removed large sections of eelgrass to investigate sources of variability of habitat use in juvenile cod. Specifically, I addressed the following questions: (1) Is eelgrass a preferred habitat for juvenile cod?; (2) Does the association of juvenile cod with habitat occur during or after settlement?; and, (3) Are patterns of habitat use similar between two congeneric species?

MATERIALS AND METHODS

Study Species

Juvenile age 0 *G. morhua* and *G. ogac* are found throughout Newfoundland nearshore coastal waters from August to late December (Methven & Bajdik 1994, Gotceitas et al. 1997, Grant & Brown 1998a). Both species are similar in appearance at early life stages (<100 mm SL) but can be distinguished in the field using lateral line characteristics (Methven & McGowan 1998) and pigment patterns. Age 0 juvenile *G. ogac* tend to be more olive in appearance whereas age 0 *G. morhua* are more golden (Laurel & Gregory, pers. obs.).

The reproductive life histories differ between the two species. *G. ogac* spawn early (Feb-Mar), have demersal eggs and spawn in the nearshore (Scott & Scott 1988). *G. ogac* are considered demersal and non-schooling residents of the nearshore throughout their life (Mikhail & Welch 1989). In contrast, *G. morhua* spawn later (Mar-Apr), have pelagic eggs and spawn in deep water both offshore (Templeman 1979) and inshore (Smedbol et al.1998). Eggs, larvae and pre-settling juveniles of *G. morhua* are transported to the nearshore, where they eventually settle from the pelagia. The two species co-occur as demersal juveniles.

Study Area

Newman Sound is a moderately sized (*ca.* 45 km^2) protected fjord of Bonavista Bay, Newfoundland located adjacent to Terra Nova National Park (TNNP; Fig. 1). Tidal amplitude in the sound is relatively low (1-1.5m) and temperatures vary seasonally from 18.0° C in August to -1.5° C in late December. Eelgrass is the dominant vegetative

nearshore habitat, found extensively along the western and southern shores of the sound. Unvegetated mineral substrates are found throughout the sound, comprising the majority of habitat along the northern shore.

Experimental Design

We selected 12 sites- 8 "eelgrass" (eelgrass+mud/silt) and 4 "non-eelgrass" (mud/sand) along southern and eastern sections of Newman Sound (Fig. 1). Eelgrass was removed at two "eelgrass" sites (Buckley's Cove-BC and Dockside-DS) and artificial eelgrass was added to two "non-eelgrass" sites (Canning's Cove-CC and Mt. Stamford-MS). Remaining unmanipulated "eelgrass" and "non-eelgrass" sites (6 and 2 respectively) were used as controls.

Habitat removal was accomplished by scuba divers in mid-July 1999, approximately two weeks prior to juvenile cod settlement. Divers marked each site with highly visible transect lines at 1 m intervals over a 500 m^2 area. Eelgrass was harvested between lines by breaking stems away from the rhizome at the base of the substrate. The process was repeated until the entire eelgrass canopy was removed in the 500 m^2 area at each site.

Artificial eelgrass was constructed for two sites, by attaching green, plastic ribbon (W: 0.8 cm H: 75.0 cm) to galvanized wire fencing. Ribbon densities fell within the range of eelgrass naturally occurring in Newman Sound i.e. 600 blades m^{-2}. A total of 80 m^2 artificial eelgrass was created for each enhancement site, and this was divided into a series of smaller patches to mimic the fragmented characteristics of natural eelgrass. Two replicates of five patch sizes (0.3, 1.1, 5.5, 11, 22 m^2) were deployed at

both CC and MS, covering a total area of 275 m^2 at each site (Fig 2). Patches were spaced 2-3 m apart and secured to the seafloor with 25 cm rebar spikes by divers. Fish were allowed to settle on artificial eelgrass patches for a period of two weeks before the sampling protocol was initiated. Patches were removed in November 1999 and redeployed in July of 2000 to prevent potential ice-scour damage.

Juvenile cod sampling

A 25 m demersal seine net with 19 mm stretched mesh size was used to collect fish over all sampling sites. The net was deployed from a small boat 50 m from shore and retrieved to shore by two individuals standing 16 m apart. The seine sampled 880m^2 of habitat from the substrate to 2 m into the water column and has been shown to have a capture efficiency of 95% (Gotceitas et al. 1997). I made a series of underwater observations in 1999, using scuba, over all of the substrates, and confirmed entire sites were sampled and fish in the path of the seine did not escape capture. Fish caught in the seine were transferred to holding containers with seawater, identified, measured to the nearest mm SL (standard length) and then returned alive to the original site of capture. Juveniles were considered "pre-settled" if SL was < 60 mm and "post-settled" if SL was ≥ 60 mm (Templeman 1966, Fahay 1983, Methven and Bajdik 1994, Tupper and Boutilier 1995a, 1995b). I used the term 'pre-settled' to describe a juvenile cod early in the transition from pelagic to demersal life (synonymous terms include, 'recently settled' – Grant and Brown 1998ab; and, 'newly settled' – Tupper and Boutilier 1995a). My choice of terminology was intentional since juvenile cod do not have a distinct settlement point and individuals larger than 60 mm SL may continue to forage on semi-pelagic prey

such as calanoid copepods (Grant and Brown 1998a, Lomond et al. 1998). However, the seine I used samples the lowermost 2 m of the water column (i.e., near the bottom), and would capture only those juvenile cod that were likely associated with the demersal habitat. All sites were sampled within two hours of low tide during daylight hours on a biweekly basis in both pre-manipulated years (1995, 1996, 1998) and post-manipulated years (1999 and 2000). Removal sites were also sampled in 2001 to measure long-term effects of habitat removal on juvenile cod distribution.

Additional data on juvenile cod habitat use and abundance was collected visually by two observers snorkeling over patches. Two 15 m transect lines were deployed perpendicular to shore within the seine path at two sites of each treatment (addition, removal, eelgrass, and sand; 2 x 4 = 8 total sites). Surveys were designed to control for the layout and area of artificial eelgrass patches added at experimental sites. The length and spacing between patches were marked on each transect while the survey width varied to accommodate the changing patch sizes encountered along the transect line. At artificial eelgrass sites, snorkelers changed their survey width to match the actual patch dimensions. At other sites, snorkelers changed their survey width at various points indicated by highly visible tape along the transect. Snorkelers swam with marked poles (2.8 m long) both to ensure no overlap of survey areas in the large patches by each observer, and to estimate width of "patches" at sites without artificial eelgrass. Pairs of snorkelers made a single pass over each transect lines at each site so that only areas falling within the delineated transect lines were surveyed ($80m^2$). Water clarity at sites did not restrict my observation ability within these limits. Snorkelers swam directly over patches, recording the abundance of juvenile cod within 0.5 m of each patch. Large

patches (11 m^2 and 22 m^2) exceeded the viewing capability of a single snorkeler, so these patches were assessed by both snorkelers swimming in parallel. Location and abundance of age 0 cod were recorded on underwater slates. I was often unable to distinguish between the smallest *G. ogac* from *G. morhua* underwater even when within 1 m. Therefore, I pooled the juvenile cod observations from snorkel surveys as *Gadus* spp. I surveyed the sites approximately weekly (n=9) between 10 August and12 October 2000 (total of 144 transect surveys).

Data Analysis

Catch data were analyzed using randomized intervention analysis (RIA) to test whether a significant change in fish density occurred after the habitat manipulation. A full description of RIA and its utility for detecting treatment effects has been reviewed by Carpenter et al. (1989). RIA is based on a before-after-control-impact (BACI) design model in which experimental and control sites are compared against each other both before and after any experimental intervention. Removal sites (n=2) were compared against natural eelgrass sites (n=6); artificial eelgrass sites (n=2) were compared against naturally unvegetated sites (n=2). RIA tests were performed on data from individual and combined years in all possible experimental-control site comparisons. However, combined years (1999-2001) were not included in the analysis of removal sites because annual regrowth at each site effectively changed the treatment over time. Catch data were transformed ($y=Log_{10}(x+1)$) prior to RIA to control for high within-site catch variability within and between years. Each RIA calculated differences between fish abundance at control and manipulated sites during each survey period. The mean of

these differences both before ($\bar{E}_{Prc}$) and after the experimental manipulation ($\bar{E}_{Post}$) was used to generate the test statistic $\bar{E}_{Dif}$ from the equation [$\bar{E}$ (PRE) - $\bar{E}$ (POST)]. The test statistic was then compared against 5000 random permutations of [$\bar{E}$ (PRE) - $\bar{E}$ (POST)] using the data of each control-experimental site comparison. The error distribution was self-derived from the randomization and therefore data did not have to meet the assumptions of normality.

RESULTS:

Juvenile age 0 *G. morhua* settled in two pulses- the first pulse in late August, the second approximately 30 days later (Fig. 3). *G. ogac* settled in a single pulse at the beginning of August (Fig. 4). Interannual variation in abundance of *G. morhua* was high between 1999 and 2000 (Fig 3), almost an order of magnitude higher in 1999 (n=6405) than in 2000 (n=845). *G. ogac* abundance varied little between 1999 (n= 8985) and 2000 (n=6614), but was higher than *G. morhua* in all years.

The distribution of pre- and post-settled cod differed between habitat, species and year. Pre- and post-settled cod (<60 mm SL) of both species were present in all habitats in 1999, but were not present at sand sites in 2000 (Fig 3; Fig 4). Differences in the abundance of post-settled *Gadus morhua* caught in natural eelgrass and removals sites were more apparent in the first year of the removal (1999) than in later years. However, post-settled *Gadus ogac* were seldom caught in the removal sites during both years.

Snorkelers observed juvenile cod within the artificial eelgrass in early August, approximately 2 weeks after patches were deployed. *Gadus* spp. were detected only in natural and artificial eelgrass sites at the time of settlement for both the first pulse (Aug

10-30) and second pulse (Oct 1-12; Fig 5). Lower numbers of cod were observed in the removal sites and these fish were often seen along the edge area of the removal. Almost no cod were sighted over open sand areas (< 0.1% of all observations).

The RIA of catch data indicated a positive change in cod abundance to the artificial eelgrass, but the magnitude of the response differed between species and years. Differences were attributed to high catch variability at one unvegetated control site, Little South Broad Cove (LSB), rather than an absence of cod at the artificial eelgrass sites (Fig 3; Fig 6). In combined years (1999 and 2000), there was a significant increase in *G. ogac* abundance at artificial eelgrass sites in all comparisons. In contrast, increases of *G. morhua* at the artificial eelgrass sites were significant in comparisons with the unvegetated control site Newbridge Cove (NB; Table 1; Fig 6). However, the trends were similar between species in individually analyzed years. Seine catches of *G. ogac* and *G. morhua* were higher at artificial eelgrass sites relative to unvegetated control sites in 50% of comparisons in 1999 and 100% in 2000 (Table 1).

G. ogac and *G. morhua* also responded differently to eelgrass removal, although both species showed signs of recovery towards the end of the experiment. Mean abundance of cod was lower in nearly all control site comparisons in all years following the removal of eelgrass (Table 2). In the first year of removal (1999), 50% and 75% of comparisons indicated a significant decline in abundance of *G. morhua* and *G. ogac* respectively (Table 2; Fig 7; Fig 8). In 2000, 16.7% of *G. morhua* and 50% of *G. ogac* comparisons were significantly lower than historic levels. However, in the final year (2001), with the exception of one *G. morhua* comparison, fish abundance generally recovered to previously observed levels (1995-1998).

DISCUSSION:

Eelgrass benefits juvenile fish by reducing predator risk (Linehan et al.2001, Laurel et al. 2003), increasing food availability (Connolly 1994), improving water quality and reducing physical exposure (Orth et al. 1984). However, juvenile fish may be distributed independent of habitat quality. Differential planktonic supply (Bell & Westoby 1986, Caselle & Warner 1996, Jenkins et al.1997a, Jenkins et al. 1998), competitive interactions (e.g. Sweatman 1985) or indiscriminate settlement patterns (Tupper & Boutilier 1995a) are known to influence spatial distribution. Therefore, proposed mechanisms of habitat use in juvenile cod have been equivocal, despite frequent observations of cod-eelgrass associations in the field (Morin et al.1991, Gotceitas et al.1997, Grant & Brown 1998ab). My study experimentally demonstrated that differential habitat-use in age 0 juvenile cod is, in part, behaviourally mediated. Juvenile cod appeared to differentiate between habitat of varying quality and preferentially occupied eelgrass areas where growth and survival were potentially highest.

Prior to the habitat manipulation, settling cod (<60 mm SL) were restricted to areas with natural eelgrass. However, following the deployment of artificial eelgrass, pre-settling *G. ogac* and *G. morhua* were caught in seines at sites historically unoccupied. These data suggest that passive planktonic supply over non-eelgrass areas was not limiting prior to the deployment of artificial eelgrass, but rather, cod were delaying settlement until preferential habitat was encountered. Although active habitat selection from the pelagia has been reported in other fish species (e.g. Marliave 1977, Sale 1984,

Levin 1991), these data contradict other published accounts of settlement in cod. In a one-year study, Tupper & Boutilier (1995a) described an indiscriminate settlement pattern in *G. morhua* across habitats of varying complexity. In their study, differences in abundance of cod between habitats occurred after settlement. They suggested that this was a result of differential predator-induced mortality rather than habitat selection. I found no evidence suggesting indiscriminate settlement in five of the six years of the catch data (1995, 1996, 1998, 2000 or 2001). However, in the year of highest overall juvenile cod abundance (1999), pre-settled cod were caught at all sites, supporting the observations of Tupper and Boutilier (1995a). Their study also indicated high densities of "newly settling" *G. morhua* (i.e., > 0.5 fish m^{-2}) at many of their sites. Only in 1999 were densities of *G. morhua* similar to those of Tupper and Boutilier (1995a; *c.* 0.3 fish m^{-2}) observed in the present study. Although comparing densities between studies can be problematic, it is possible that settlement patterns in cod were density-dependent (e.g., Myers and Cadigan 1993; Fromentin et al. 2001). In high abundance years, apparent habitat quality may decrease through saturation effects (e.g., competition for space, prey, or resources), leading to settlement in suboptimal habitats.

The proximal cause of the disappearance of pre-settling fish from unstructured and removal sites in the present study is unknown. However in another study (Laurel et al. In press, Chapter 3), I have demonstrated that juvenile cod exhibit increased aggregation behaviour and increased tendency to move under conditions of high density when they occupy unstructured habitat, compared to low density, when they did not occupy such habitat. Such behaviour may be a means of compensating for increased predator risk associated with life in unstructured habitats.

An alternative explanation is that settling cod (<60 mm) initially settled in natural eelgrass sites and shortly thereafter moved to artificial eelgrass sites. However, I suggest this was unlikely for a number of reasons. First, at all sites, a migration of >1 km across deep or unvegetated habitats would be required to occupy artificial eelgrass sites from natural eelgrass sites. Such a migration would be improbable because risk of predation in juvenile cod increases with water depth (Linehan et al. 2001) and with declining structural complexity (Gotceitas et al. 1996, Laurel et al. 2003). In addition, the susceptibility of juvenile fish to predators is known to be size-dependent (Sogard 1997). Therefore the risk of movement among safe habitats at small body sizes would likely be prohibitive. Finally, a recent study analyzing patchiness of demersal *G. morhua* within nearshore areas suggests that movement of small pre-settling cod (25-40mm) is less than that in larger, post-settled fish (Methven et al. 2003). Therefore, in my study, the distribution of small cod (< 60 mm SL) was likely the result of settlement from the pelagia rather than movements between demersal habitats.

Substantial movement more likely occurred in larger, post-settled juvenile cod. High within-site variation suggested that post-settled cod were not restricted to the area in which they settled. The high catch variation within manipulated sites also suggested that post-settled fish move among habitats. Sogard (1989) also demonstrated that many settled juvenile fish species move long distances (*ca.* 4 km) to occupy artificial seagrass patches. Neither Sogard (1989) and nor my data support Bell and Westoby's (1986) "settle and stay" hypothesis. Bell and Westoby (1986) suggested juvenile fish settle indiscriminately within a habitat but may move within that habitat for microsite selection. However, my observations are neither consistent with "settle and stay" nor do they

suggest cod exhibit strong site fidelity. Tupper & Boutilier (1995a, 1995b) have argued that juvenile cod are strongly site-attached and shifts in the observed abundance of settled fish is exclusively due to mortality. In these two studies, juvenile *G. morhua* (60-100 mm SL) were observed defending small territories and having limited, size-dependent home ranges (<100 m^2) for 2-3 months following settlement. My survey methods encompassed these reported home-ranges, yet snorkel observations and seine catches were highly variable between sampling periods. I do not attribute observed variation to mortality alone since density of post-settled individuals often increased within a site through the season. Therefore it would appear that both cod species were mobile at scales greater than *ca.* 1000m^2. Whether these movements were unrestricted or fell within an established home range could not be determined. My results were consistent with Sogard (1989) and do not support the "settle and stay" hypothesis advocated by others (e.g. Bell & Westoby 1986, Tupper & Boutilier 1995a,1995b) for juvenile cod.

Both cod species altered their distribution following the habitat manipulation, but their habitat use patterns were not identical. *G. ogac* abundance decreased in more removal-eelgrass control comparisons than *G. morhua*, suggesting that *G. ogac* is more sensitive to alterations in habitat complexity. Yet despite an overall preference for eelgrass, *G. morhua* were periodically caught over sand and removal sites, suggesting that habitat use in this species is more flexible at early life stages. These differences may reflect different spawning characteristics between the two species. *G. ogac* spawn demersal eggs (Scott & Scott 1988) in close proximity to nursery areas whereas *G. morhua* spawn pelagic eggs, often further offshore (Templeman 1979). Larvae from demersally spawned eggs are more likely to be retained in the area spawned relative to

pelagic eggs (Bradbury et al. In press). Conversely, pelagic eggs have a greater dispersal potential than demersal eggs due to a prolonged planktonic development (Bradbury et al. 2000). Thus there is greater likelihood that settling *G. morhua* will have fewer opportunities to settle in eelgrass habitat than *G. ogac*. Consequently, age 0 *G. morhua* may have evolved a greater tolerance for the use of alternative habitats, such as gravel-cobble (Lough et al.1989) and rocky reefs (Tupper & Boutilier 1995a).

The RIA measured a relative effect on fish abundance rather than a shift in absolute abundance. Largely, this was done to control for individual site-differences (e.g. eelgrass biomass, patchiness, planktonic supply) that could contribute to differential abundance of cod within a habitat treatment. In addition, the artificial eelgrass may not completely mimic natural eelgrass i.e. the additional structure from the wire base, lack of natural die-off, etc. However, the logistical constraints of carrying out a large-scale habitat manipulation did not permit us to manipulate habitat at an equivalent area to natural eelgrass control site. Therefore, absolute comparisons would be inappropriate regardless of possible inherent site differences. Therefore, the high abundance of juvenile cod, namely *G. morhua*, at removal sites was not unexpected. Thirty-five percent of each removal site still contained undisturbed eelgrass, although this was only in the shallow intertidal zone where few juvenile fish are found regardless of habitat characteristics (Jenkins et al. 1997b), including *Gadus* spp. (Norris et al. in revision). Another source of juvenile cod in the removal sites were the edges along the subtidal boundary of the removal. I observed schools of juvenile cod along the deeper edge of the removal sites where the manipulated area adjoined undisturbed eelgrass, but I rarely observed cod over the interior of the removal. Edge areas in eelgrass are known to be

profitable foraging areas for fish (Graham et al. 1998) and it is possible that edge-associated fish contributed substantially to the seine catches. In addition, removal sites may have had higher prey levels than sand sites. Although the response of macroinvertebrates to alterations in seagrass is species and site-specific (e.g. Edgar & Robertson 1992, Connolly & Butler 1996, Lee et al. 2001), Connolly (1994) found higher overall invertebrate abundance in small removal areas (25 m^2) compared to naturally unvegetated areas. In this study, I removed the canopy of eelgrass and left the rhizomes intact in the benthos. Potentially, the procedure left a rich benthic invertebrate community relative to naturally unvegetated sites.

In a few instances, the highest numbers of juvenile cod were caught in artificial eelgrass sites. This was interesting considering that the eelgrass coverage at artificial sites (275 m^2) was substantially less than natural sites (880 m^2). The visual transect data, which controls for habitat area, also confirmed that overall cod abundance was higher in the artificial eelgrass. These results may demonstrate an "oasis effect" since artificial eelgrass sites were further removed from natural eelgrass patches than natural eelgrass sites. Assuming fish seek the most proximate refuge, patches of suitable habitat may be colonized at high rates when surrounded by large areas of unsuitable habitat (Virnstein & Curran 1986). Other studies have shown that higher densities of fish are found in isolated patches of eelgrass (Sogard 1989) and reef habitat (Schroeder 1987) when compared to continuous eelgrass meadows. Similar findings have also been reported for cod. Eelgrass sites with slight fragmentation supported higher densities of age 0 juvenile cod than eelgrass meadows of equivalent area (Wells 2002). My results were consistent with these findings.

Appreciable regrowth of eelgrass at the removal sites occurred two years following its initial removal. This regrowth was reflected in the number of significant RIA removal-control site comparisons. In the first year of removal (1999), nearly 50% of the RIA comparisons indicated a significantly lower juvenile cod abundance in removal sites compared to years prior to the removal. By 2001, differences between removal and vegetated sites were no longer significant. Eelgrass reproduces both sexually and asexually (Orth et al. 1984). The close proximity of undisturbed eelgrass to the removal areas also likely facilitated the quick recovery. A larger, more geographically isolated removal location or a complete removal of canopy, including rhizomes (which I left largely intact) may have had longer-term effects on juvenile cod distribution.

CONCLUSIONS

Both *G. ogac* and *G. morhua* abundance increased at sites enhanced with artificial eelgrass and decreased at sites where eelgrass was removed, relative to years before I manipulated habitat. Therefore, I reject the hypothesis that broad-scale processes (e.g., larval supply and oceanographic hydrodynamics) were responsible for the differential use of vegetated and unvegetated habitats. The presence of settling cod over sites with artificial eelgrass in years of high and low abundance suggests that these species are capable of selecting habitat while still in the pelagia.

Both species exhibited an overall preference for eelgrass habitat. However, high within-site variability indicated that both species are not strongly site-attached. High catch variability was especially evident in *G. morhua*. Significant RIA comparisons were fewer in *G. morhua* relative to *G. ogac*, suggesting that *G. morhua* were less site-attached

or less dependent on habitat complexity than its sibling species. These data contradict Tupper and Boutilier's (1995ab) accounts of cod settling indiscriminately across a range of habitats and having high site-fidelity following settlement.

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FIGURE CAPTIONS:

Fig. 1: Study area in Newman Sound, Bonavista Bay, Newfoundland showing the locations of experimental and reference seine locations. ●= eelgrass sites Big Brook (BB), Hefferen's Cove (HC), Minchin's Cove (MC), Mistaken Cove (MI), South Broad Cove (SB) and White Rock (WR); ■= artificial eelgrass sites Canning's Cove (CC) and Mt. Stamford (MS); ○= unvegetated sites Little South Broad Cove (LSB) and Newbridge (NB); □= removal sites Buckley's Cove (BC) and Dockside (DS).

Fig. 2: Experimental layout of artificial eelgrass patches relative to shore at Mt. Stamford and Canning's Cove.

Fig. 3: Interannual pre- and post-settlement distribution (catch per haul) of age 0 *Gadus morhua* in experimental and reference sites for July-Dec in 1999 and 2000. Values are means of seine hauls at replicate sites (n=2-6) ± S.E.

Fig. 4: Interannual pre- and post-settlement distribution (catch per haul) of age 0 *Gadus ogac* in experimental and reference sites for July-Dec in 1999 and 2000. Values are means of seine hauls at replicate sites (n=2-6) ± S.E.

Fig. 5: Visual observations of age 0 juvenile cod *Gadus* spp. abundance over a nine week period (Aug 12-Oct 12) at eelgrass, removal, unvegetated sand and artificial eelgrass sites. Values are means of replicate transect lines (n=4) ± S.E. Points at each week are staggered (0.1 weeks) for visual purposes.

Fig. 6: Relative differences of juvenile cod abundance, (*Gadus morhua* and *G. ogac*) at artificial eelgrass sites (Canning's Cove-CC and Mount Stamford-MS) and unvegetated reference sites (Newbridge-NB and Little South Broad Cove-LSB) during pre- and post-manipulation years. Values represent annual mean bi-weekly seine catches (n=14-20) ± S.E. Points at each year are staggered (0.05 yrs) for visual purposes.

Fig. 7: Relative differences of juvenile cod abundance *Gadus morhua*, at experimental removal sites (Buckley's Cove-BC and Dockside-DS) and natural eelgrass reference sites (Big Brook-BB, Hefferen's Cove-HC, Minchin's Cove-MC, Mistaken Cove-MI, South Broad Cove-SB and White Rock-WR) during pre- and post-habitat manipulation years. Values represent annual mean bi-weekly seine catches (n=14-20) ± S.E. Points at each year are staggered (0.05 yrs) for visual purposes.

Fig. 8: Relative differences of juvenile cod abundance *Gadus ogac*, at experimental removal sites (Buckley's Cove-BC and Dockside-DS) and natural eelgrass reference sites (Big Brook-BB, Hefferen's Cove-HC, Minchin's Cove-MC, Mistaken Cove-MI, South Broad Cove-SB and White Rock-WR) during pre- and post-habitat manipulation years. Values represent annual mean bi-weekly seine catches (n=14-20) ± S.E. Points at each year are staggered (0.05 yrs) for visual purposes.

Fig. 1

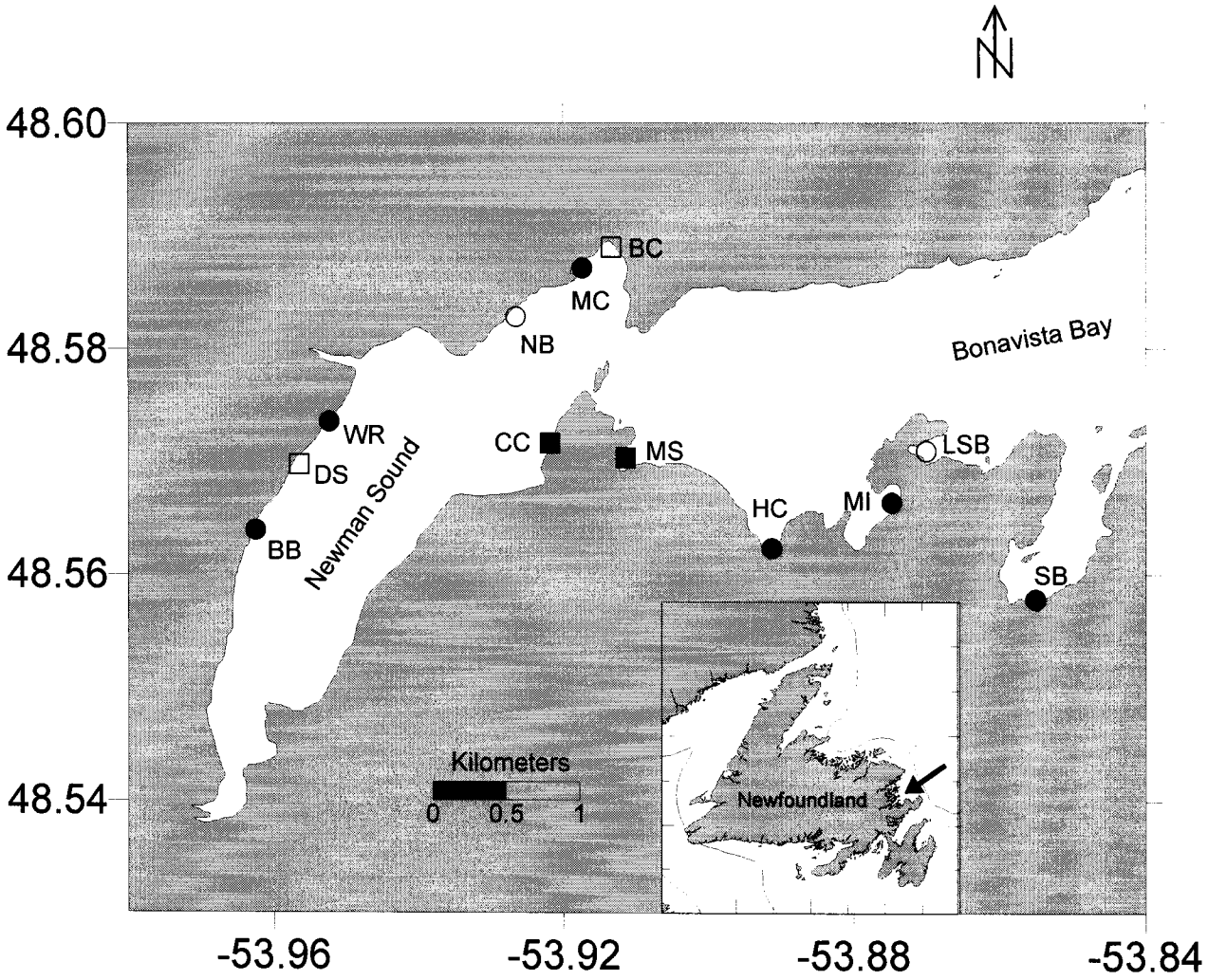
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Fig. 2

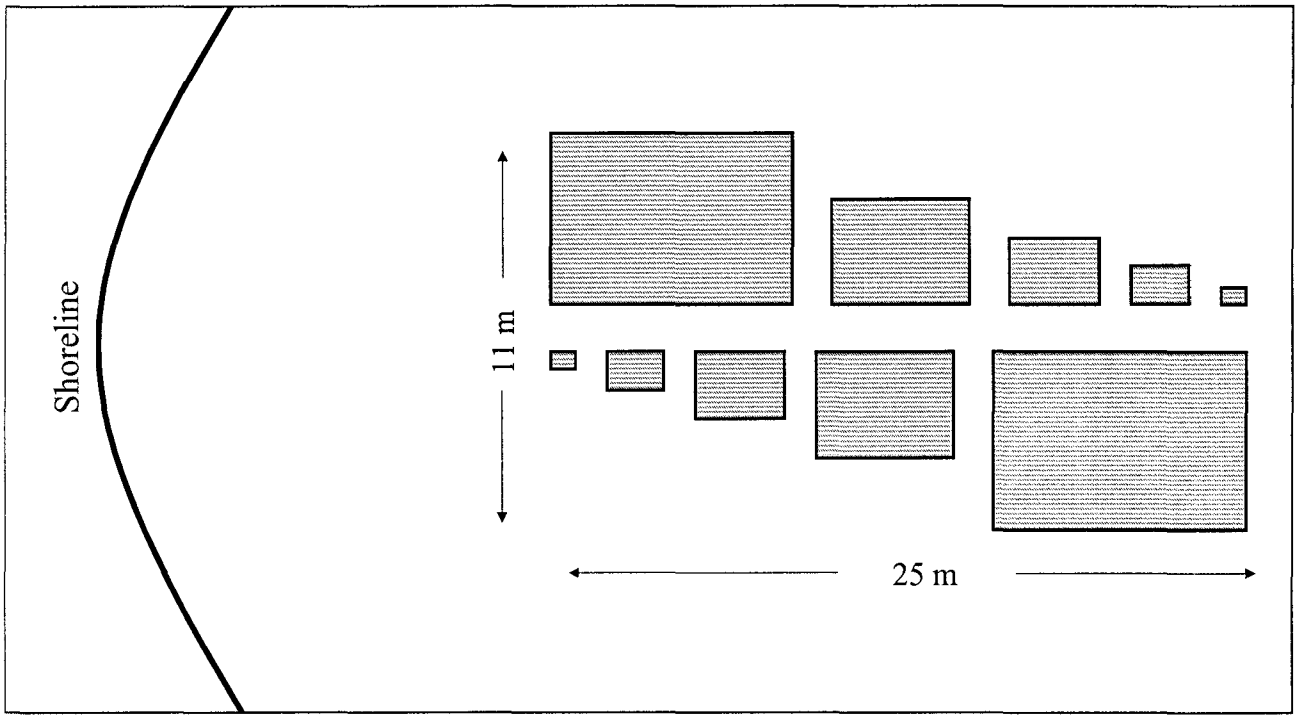

Fig. 3

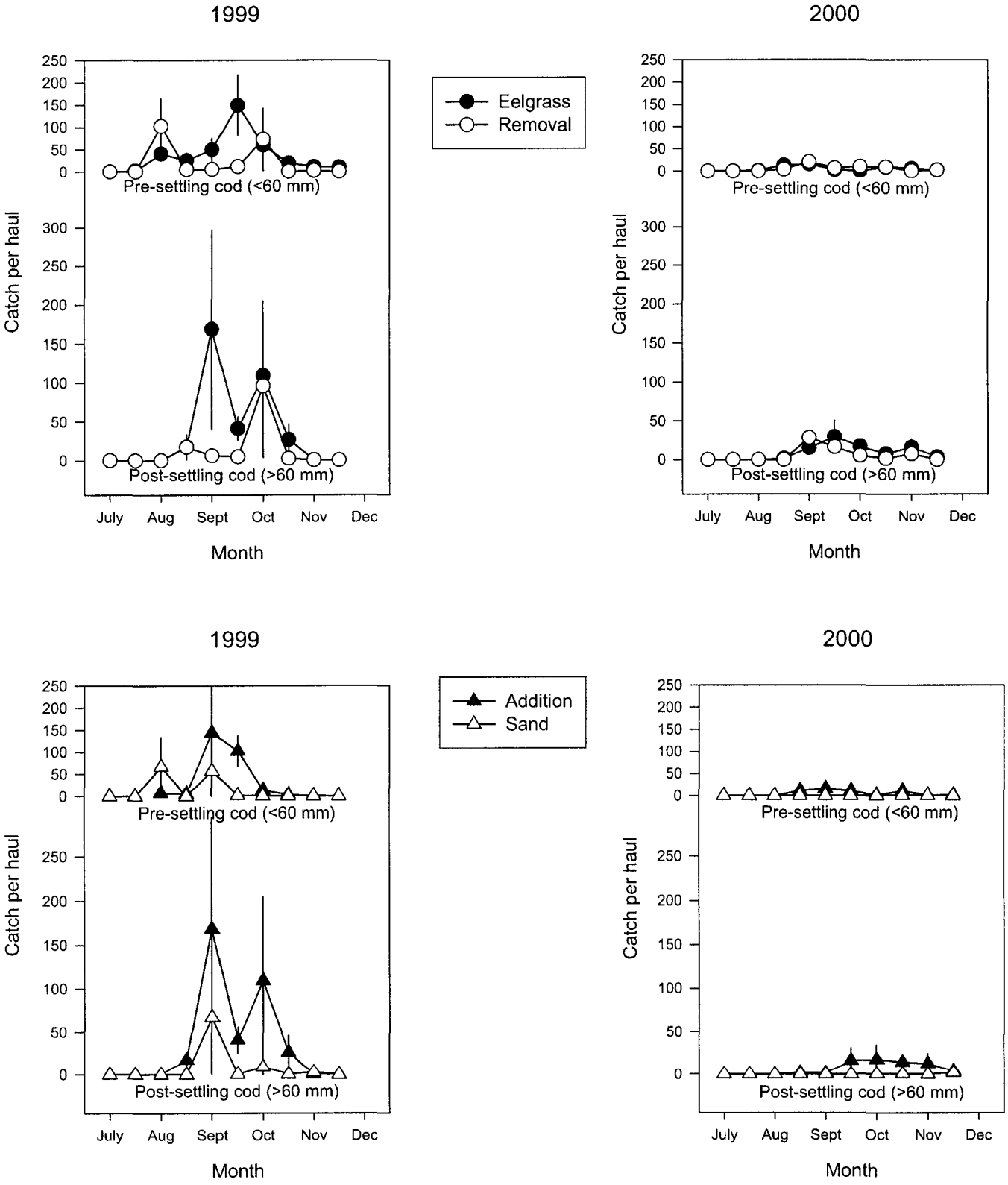
1999
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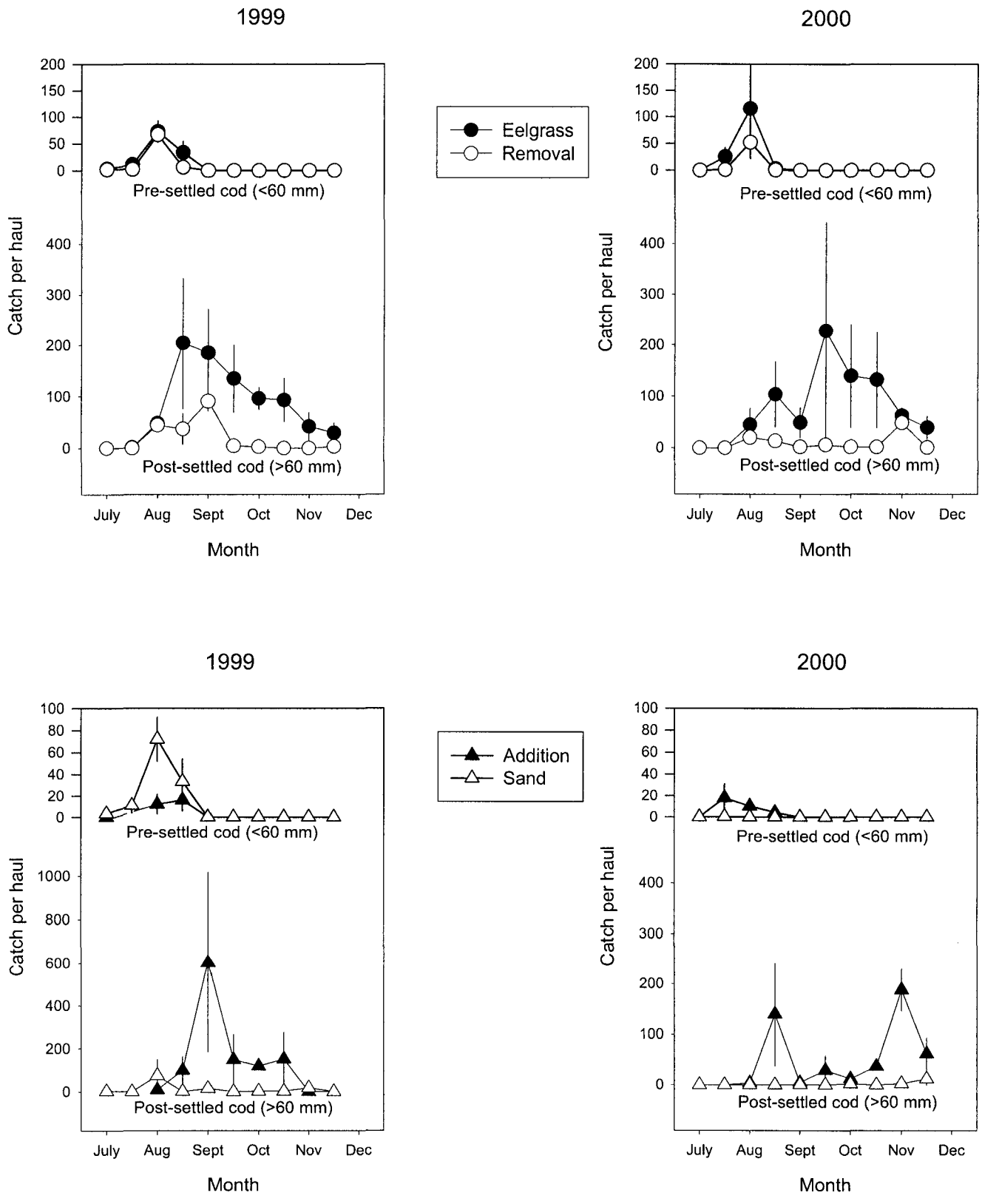
Fig. 4


1999
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Eelgrass
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Pre-settled cod (<60 mm)
Post-settled cod (>60 mm)
Catch per haul
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Month

Fig. 5

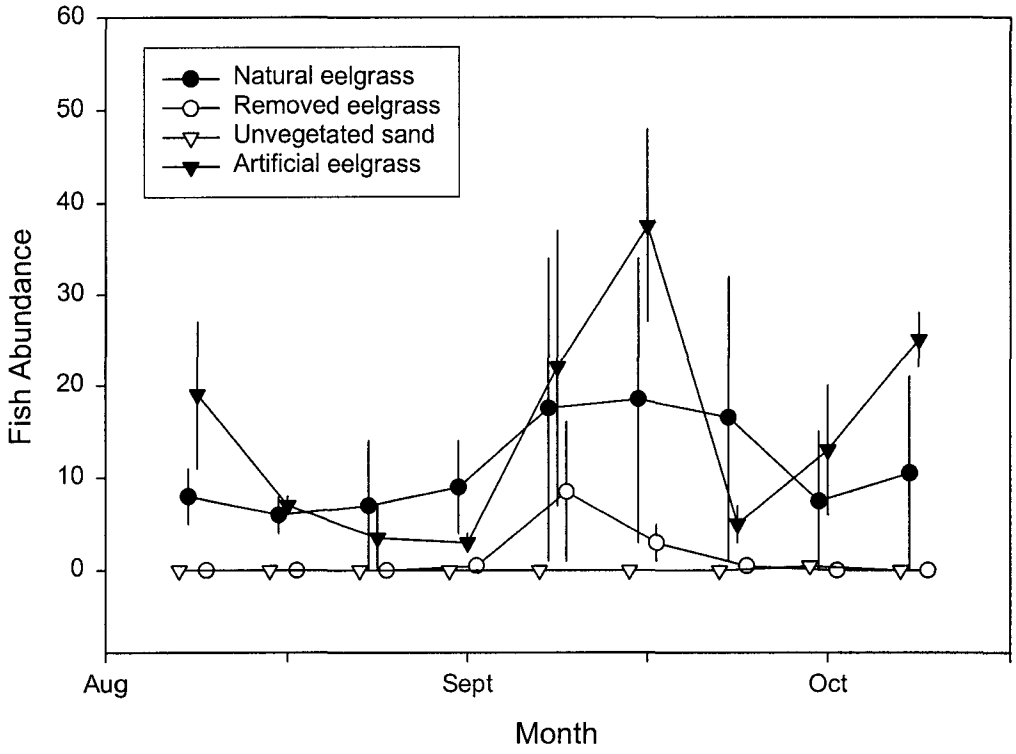

60
50
40
30
20
10
0
Fish Abundance
Natural eelgrass
Removed eelgrass
Unvegetated sand
Artificial eelgrass
Aug
Sept
Oct
Month

Fig. 6

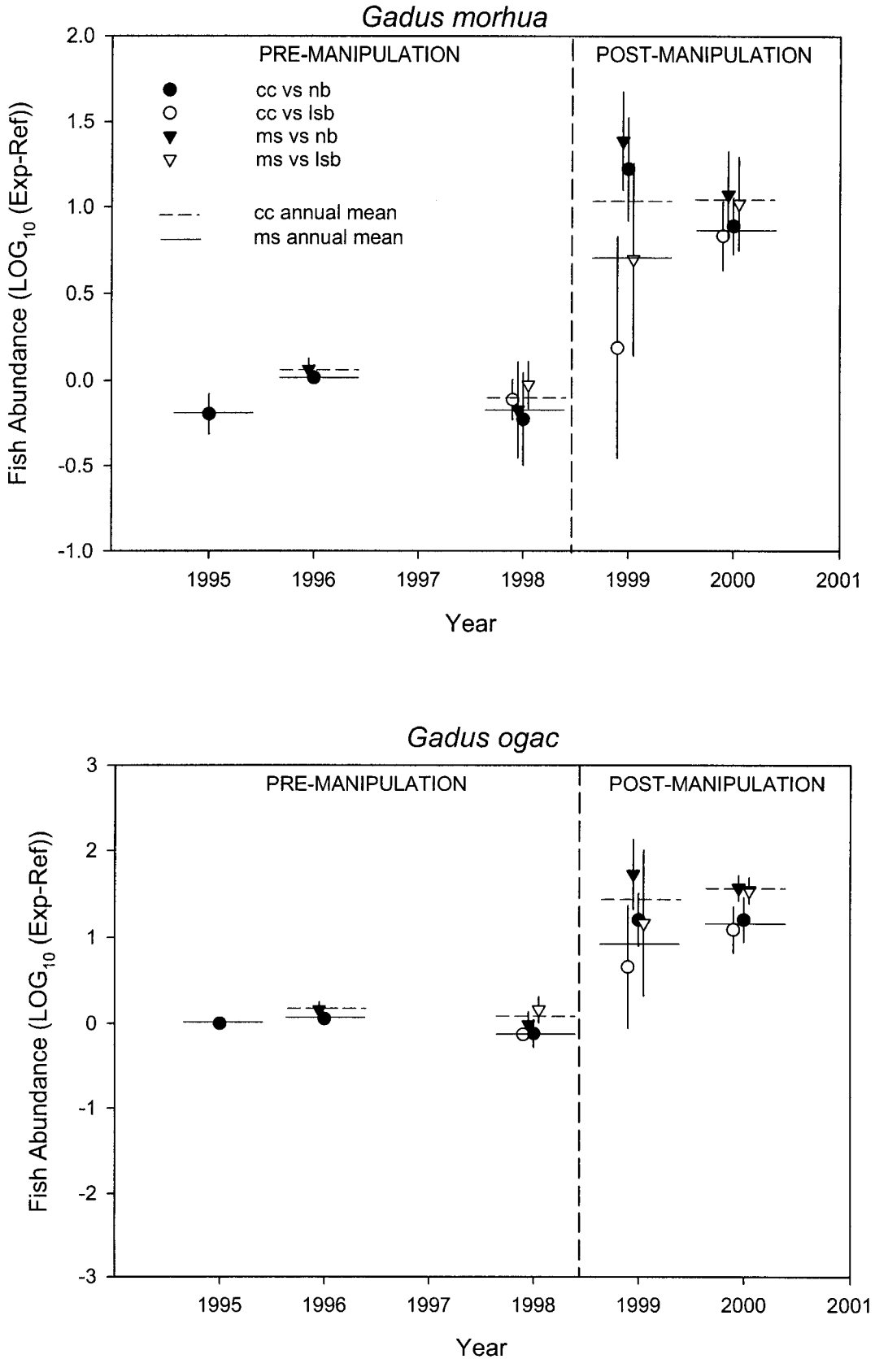
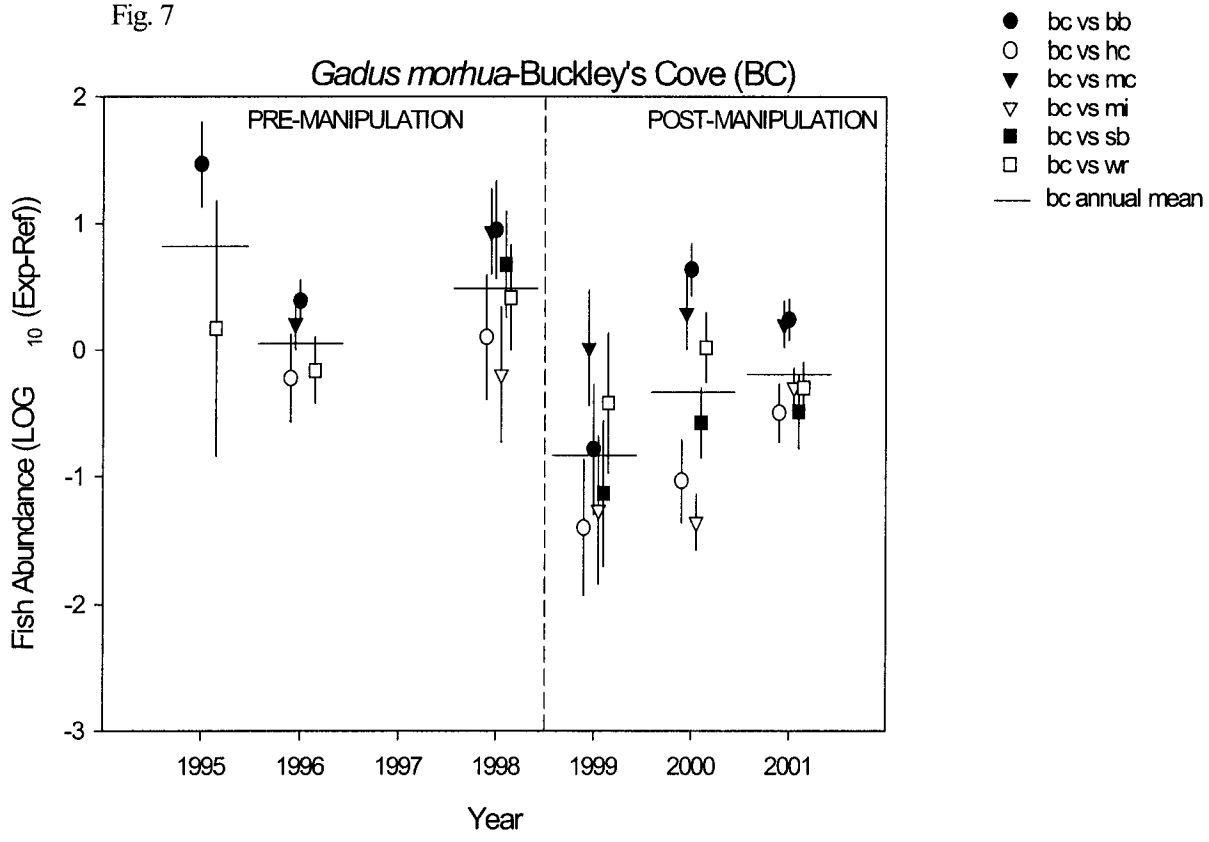

Gadus morhua
PRE-MANIPULATION
POST-MANIPULATION
cc vs nb
cc vs lsb
ms vs nb
ms vs lsb
cc annual mean
ms annual mean
Fish Abundance (LOG10 (Exp-Ref))
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
1995
1996
1997
1998
1999
2000
2001
Year
Gadus ogac
PRE-MANIPULATION
POST-MANIPULATION
Fish Abundance (LOG10 (Exp-Ref))
3
2
1
0
-1
-2
-3
1995
1996
1997
1998
1999
2000
2001
Year

Fig. 7


Gadus morhua-Buckley's Cove (BC)
PRE-MANIPULATION
POST-MANIPULATION
Fish Abundance (LOG 10 (Exp-Ref))
Year
1995
1996
1997
1998
1999
2000
2001
2
1
0
-1
-2
-3
bc vs bb
bc vs hc
bc vs mc
bc vs mi
bc vs sb
bc vs wr
bc annual mean

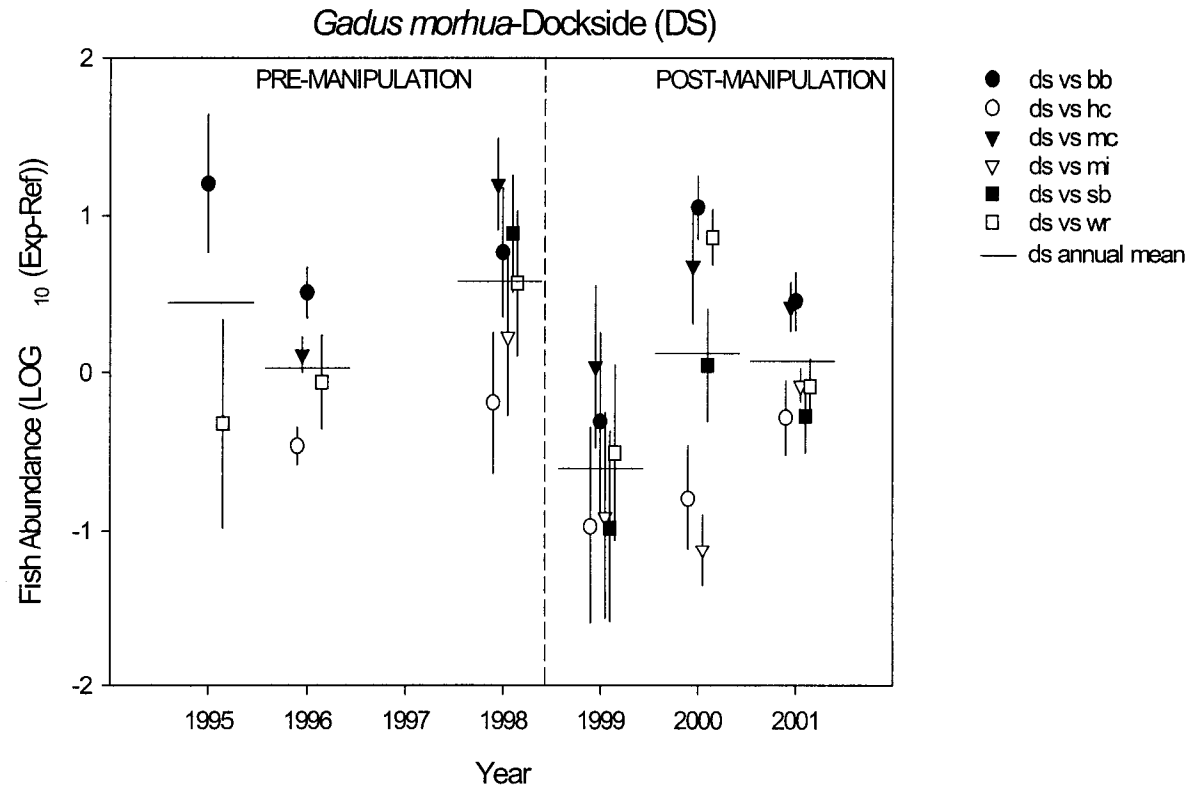
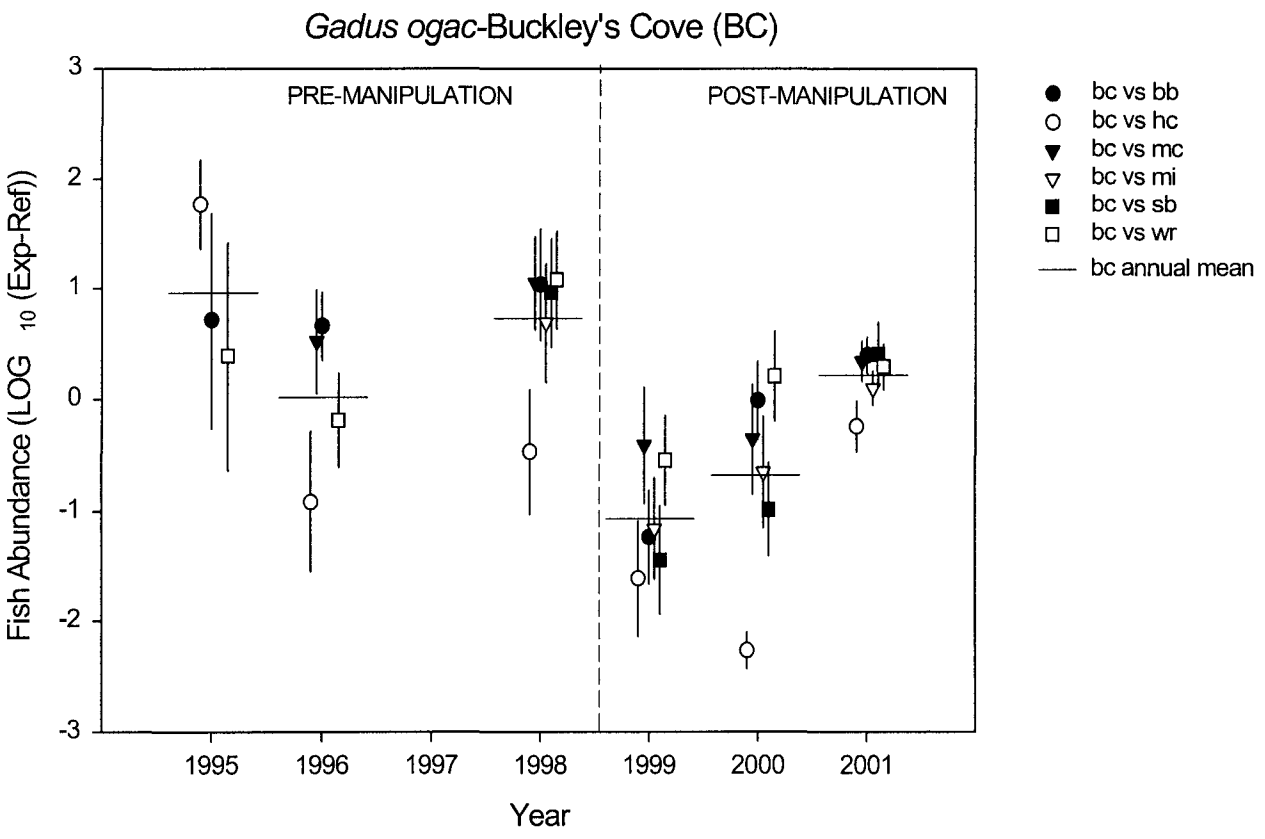

Gadus morhua-Dockside (DS)
PRE-MANIPULATION
POST-MANIPULATION
Fish Abundance (LOG 10 (Exp-Ref))
Year
1995
1996
1997
1998
1999
2000
2001
2
1
0
-1
-2
ds vs bb
ds vs hc
ds vs mc
ds vs mi
ds vs sb
ds vs wr
ds annual mean

Fig. 8


Gadus ogac-Buckley's Cove (BC)
PRE-MANIPULATION
POST-MANIPULATION
Fish Abundance (LOG 10 (Exp-Ref))
Year
1995
1996
1997
1998
1999
2000
2001
3
2
1
0
-1
-2
-3
bc vs bb
bc vs hc
bc vs mc
bc vs mi
bc vs sb
bc vs wr
bc annual mean

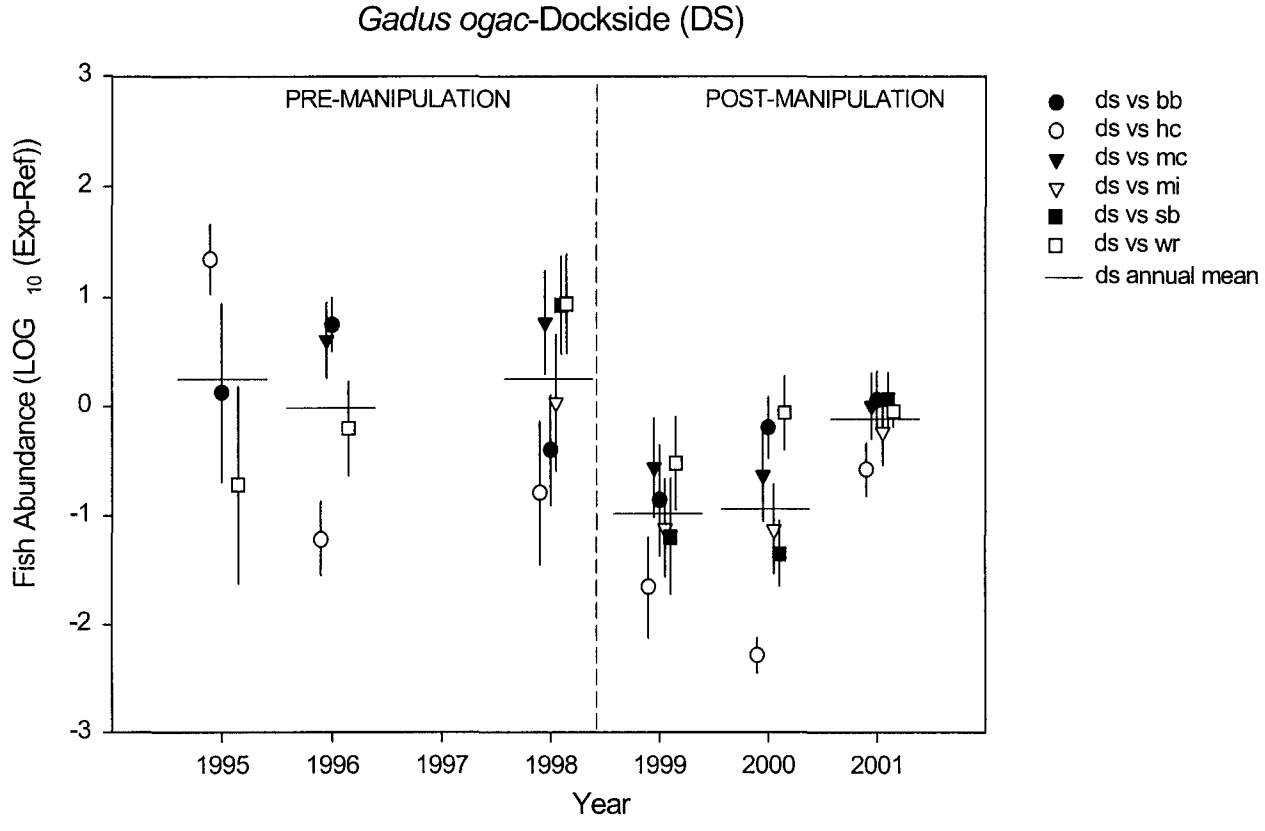

Gadus ogac-Dockside (DS)
PRE-MANIPULATION
POST-MANIPULATION
Fish Abundance (LOG 10 (Exp-Ref))
Year
1995
1996
1997
1998
1999
2000
2001
3
2
1
0
-1
-2
-3
ds vs bb
ds vs hc
ds vs mc
ds vs mi
ds vs sb
ds vs wr
ds annual mean

Table 1: Probability values from Randomized Intervention Analysis (RIA) of *Gadus morhua* and *G. ogac* from two artificial eelgrass sites (Canning's Cove-CC and Mount Stamford-MS) and two unvegetated reference sites (Newbridge-NB and Little South Broad Cove-LSB). (-) or (+) indicates a positive or negative effect from the removal with * denoting significance. The components $\bar{E}_{Prc}$ and $\bar{E}_{Post}$ for the test statistic $\bar{E}_{Dif}$ of each comparison are plotted in Fig. 6.

Species	Year	Site	NB	LSB
G. morhua	***1999-2000***	CC	(+) 0.001**	(+) 0.251
		MS	(+) 0.001**	(+) 0.063
	1999 only	CC	(+) 0.001**	(+) 0.670
		MS	(+) 0.001**	(+) 0.190
	2000 only	CC	(+) 0.001**	(+) 0.002**
		MS	(+) 0.001**	(+) 0.006**
G. ogac	***1999-2000***	CC	(+) 0.001**	(+) 0.041*
		MS	(+) 0.001**	(+) 0.034*
	1999 only	CC	(+) 0.002**	(+) 0.276
		MS	(+) 0.001**	(+) 0.200
	2000 only	CC	(+) 0.001**	(+) 0.001**
		MS	(+) 0.001**	(+) 0.001**

Table 2: Probability values from Randomized Intervention Analysis (RIA) of *Gadus morhua* and *G. ogac* from two experimental removal sites (Dockside-DS and Buckley's Cove-BC) and five natural eelgrass reference sites (Big Brook –BB, Hefferen's Cove-HC, Minchin's Cove-MC, Mistaken Cove-MI, South Broad Cove-SB and White Rock-WR). (-) or (+) indicates a positive or negative effect from the removal with * denoting significance. The components $\bar{E}_{Prc}$ and $\bar{E}_{Post}$ for the test statistic $\bar{E}_{Dif}$ of each comparison are plotted in Fig. 7 and 8.

Species	Year	Site	MC	MI	SB	WR	BB	HC
G. morhua	1999	DS	(-) 0.146	(-) 0.153	(-) 0.029*	(-) 0.217	(-) 0.025*	(-) 0.278
		BC	(-) 0.158	(-) 0.027*	(-) 0.017*	(-) 0.308	(-) 0.001*	(-) 0.026*
	2000	DS	(-) 0.484	(-) 0.022*	(-) 0.153	(+) 0.079	(-) 0.650	(-) 0.252
		BC	(-) 0.220	(-) 0.060	(-) 0.035*	(-) 0.794	(-) 0.373	(-) 0.058
	2001	DS	(-) 0.277	(-) 0.667	(-) 0.031*	(-) 0.560	(-) 0.462	(-) 0.964
		BC	(-) 0.175	(-) 0.852	(-) 0.055	(-) 0.296	(-) 0.099	(-) 0.304
G. ogac	1999	DS	(-) 0.024*	(-) 0.212	(-) 0.012*	(-) 0.234	(-) 0.033*	(-) 0.010*
		BC	(-) 0.032*	(-) 0.032*	(-) 0.005*	(-) 0.056	(-) 0.001*	(-) 0.033*
	2000	DS	(-) 0.022*	(-) 0.158	(-) 0.002*	(-) 0.655	(-) 0.425	(-) 0.005*
		BC	(-) 0.036*	(-) 0.115	(-) 0.015*	(-) 0.681	(-) 0.110	(-) 0.002*
	2001	DS	(-) 0.186	(-) 0.900	(-) 0.289	(-) 0.662	(-) 0.777	(-) 0.675
		BC	(-) 0.293	(-) 0.424	(-) 0.473	(-) 0.741	(-) 0.4116	(-) 0.796

CHAPTER 3:

Density-dependent habitat use in juvenile cod (*Gadus morhua*): alternative strategies in high-risk environments

ABSTRACT:

Fish behaviour can change to accommodate a variable environment, but changes in behaviour have not been considered in the context of density-dependent habitat use. In Bonavista Bay, Newfoundland, I measured how fish density, movement and schooling behaviour changed with habitat in two gadids, Atlantic cod (*Gadus morhua*) and Greenland cod (*Gadus ogac*), using a combination of field-seines, mark-recapture- and laboratory experiments. Density estimates from seines (n=427) over five years (1996, 1998-2001) indicated that these species were associated with eelgrass but periodically were detected in high abundance over sand. Within-site catch variation indicated both species aggregated more in sand than eelgrass habitat, and in Atlantic cod, aggregations over sand increased as density in eelgrass increased. Although such patterns in catch data could be interpreted as an effect of differential mortality between habitats, a mark-recapture experiment indicated that both species of cod were not site-attached and moved between seine locations. Furthermore, video-analysis from laboratory experiments demonstrated that cod formed tighter aggregations over sand compared to eelgrass habitats. My results demonstrate that juvenile cod modify their behaviour with changing density, possibly as a means of exploiting poor quality habitats when high quality habitats are saturated with conspecifics. Consequently, habitat suitability for Atlantic cod should be considered a dynamic rather than fixed variable in density-dependent habitat models.

KEY WORDS: Density-dependence · Habitat selection · Atlantic cod · Greenland cod · Aggregation · Shoaling

INTRODUCTION:

Predation in aquatic systems can have profound effects on the distribution of many species of fish (Sih 1987). Predators can shape prey fish distribution either directly through selective mortality (e.g., Tupper and Boutilier 1995a, Steele 1999) or indirectly through risk-induced behaviour such as schooling or use of protective habitat (See Godin 1997 for review). It is likely that both direct and indirect effects of predation on fish distribution are magnified during the early life stages of fish when predation risk is highest (e.g., Houde 1987, Sogard 1997).

Complex habitats (e.g., rock, woody debris, coral, submerged vegetation) are often used by fish as a means of reducing predation risk (Savino and Stein 1982, Gotceitas and Colgan 1989, Gotceitas and Brown 1993). In particular, highly structured aquatic vegetation (e.g., eelgrass) has received much attention as a refuge habitat (Orth et al. 1984, Gotceitas et al.1997, Linehan et al. 2001, Laurel et al. In press), likely due to its wide distribution and high productivity relative to neighboring unvegetated sites (Orth et al. 1984, Bell and Pollard 1989). The likelihood of encountering and capturing prey is reduced in eelgrass (Gotceitas et al. 1997), and consequently, predation rates are typically lower despite sometimes-higher predator densities in these habitats (Linehan et al.2001, Laurel et al. 2003). It is therefore not surprising that structured habitat is often used as nursery habitat by many species of recently settled marine fish (Bell and Pollard 1989, Sogard and Able 1991, Levin 1991, Edgar and Shaw 1995, Grant and Brown 1998a, Matilla et al. 1999).

Despite the benefits of using complex habitats, fish may be forced to use high-risk habitats (e.g., sand, bedrock) when preferential habitats are saturated by conspecifics. The decline in habitat selection with increasing population abundance was first outlined by Fretwell and Lucas (1970) and has subsequently formed the basis for frequency-dependent modeling i.e., ideal-free distribution. When populations are low, individuals should be restricted to habitats offering the highest fitness benefits e.g., high survival and growth. As population density increases, individual fitness benefits decrease (via competitive interactions) and consequently, poorer quality habitats become more attractive. These relationships have been explored and reviewed for many taxa, including fish (MacCall 1990, Kramer et al. 1997).

One shortcoming with density-dependent habitat models is that they assume the organism's behaviour is the same across all habitats. Such an assumption is problematic because changes in behaviour can modify the fitness benefits associated with a particular habitat. Density-dependent habitat models rely on a static measure of habitat suitability, equal to the fitness benefits acquired by an organism at zero density. The fitness benefits of a habitat cannot be static if the organism has a dynamic behavioural strategy. Therefore, density-dependent changes in behaviour should also be considered when modeling habitat suitability and predicting distribution.

Fish adopt different strategies to compensate for increased predation risk associated with specific habitats. Immediate, short-term responses include freezing (motionless) (e.g., Brown 1984, Radabaugh 1989), reduced activity (Rahel and Stein 1988) and increased flight initiation distances (Ydenberg and Dill 1986). However, employing these tactics can result in reduced mating success (e.g., Hastings 1991) and

lost foraging opportunities (e.g., Williams and Brown 1991). Alternatively, group tactics (e.g., schooling, shoaling) may be more viable long-term solutions when using poorer quality habitat. Shoaling has been shown to reduce predation risk through increased predator confusion (e.g., Milinski 1979; 1985), dilution (Foster and Treherne 1981; Krebs and Davies 1991) and vigilance (Bertram 1978). The cost of group association (e.g., food competition, increased conspicuousness) may be ameliorated by increased food searching (Pitcher et al. 1982), group defense (Krebs and Davies 1991), and increased hydrodynamic efficiency (Weihs 1975). However, the use of shoaling as an alternative tactic in habitats with low suitability has not been considered in the context of density-dependent habitat selection.

Little is known of mechanisms of variable habitat use of juvenile Atlantic cod. Since the collapse of Atlantic cod populations off Newfoundland, age 0 juvenile cod have been largely restricted to the inshore (Dalley and Anderson 1997) where they are commonly associated with complex bottom habitat (Gotceitas et al. 1997, Grant and Brown 1998a). Field experiments have demonstrated that these fish prefer to settle in eelgrass in July-August (Laurel et al. In press, Chapter 2) and remain there until late November when they presumably move to deeper waters (Methven and Bajdik 1994). Eelgrass has been shown to reduce predation risk for age 0 juvenile cod in both laboratory (Gotceitas et al. 1997) and field (Linehan et al. 2001; Laurel et al. 2003) experiments. Despite their preference for eelgrass, however, juvenile cod are occasionally observed over less structured habitats such as sand and cobble (Lough et al. 1989, Tupper and Boutilier 1995ab, Laurel et al. In press, Chapter 2). Juvenile cod are believed to move little immediately following settlement (Tupper and Boutilier 1995ab,

Grant and Brown 1998a) and consequently, the occupation of less structured habitats is taken to be the result of indiscriminate settlement patterns. By implication, temporal variation in distribution following settlement is the result of selective predation across habitats (Tupper and Boutilier 1995ab). However, Schneider et al.(1999) demonstrated that movement prevails over mortality at the scales of Tupper and Boutilier (1995ab). Furthermore, a recent study by Laurel et al. (In press, Chapter 2) suggested that temporal variation in distribution is the result of post-settlement movement and habitat mediated aggregation. Therefore, the mechanisms of variable habitat use in these fish remains unclear.

In this study I measured movement, fish density and behaviour in laboratory and field experiments to determine: 1) the degree of post-settlement movement in juvenile cod; 2) if cod behave similarly in open and vegetated habitats; and 3) whether habitat-dependent behaviour is density-dependent.

MATERIALS AND METHODS:

Study location:

Fieldwork was carried out along shallow coastal areas (< 5m) of Newman Sound, Terra Nova Nation Park (TNNP), located within Bonavista Bay Newfoundland (Fig. 1). Nearshore substrate varied between complex eelgrass (*Zostera marina*)/mud habitats to non-vegetated sand/gravel habitat. Seasonal temperatures ranged from 20° C in late August to -1.0° C in early December.

Seine surveys:

Age 0 juvenile cod abundance was determined using demersal beach seines in 1996 and 1998- 2001. Seines were deployed 55 m from shore from a 6 m boat and pulled toward shore by two individuals standing 16 m apart. The seine sampled 880 m^2 of demersal habitat up to 2 m from the bottom. Seine collections were made only during daylight hours and within 2 hrs of low tide. Fish collected in the seine were transferred to large containers filled with seawater at ambient temperature. Juvenile cod were counted and identified before being returned alive to their site of capture. Scuba observations have shown that the seine samples 95% of the fish community within its path (Gotceitas et al. 1997). A full description of the seine, mesh size and deployment method is found in Schneider et al. (1997).

In each year of my study, collections were taken once every two weeks over 2-4 unvegetated sand sites and 4-8 eelgrass sites between mid-July and late November. Nearshore studies in Newfoundland have shown that *Gadus morhua* settle in at least two distinctive recruitment pulses. The first pulse occurs in Aug-Sept which is then followed by a 2^{nd} pulse occurring approximately 30 days later (Methven and Bajdik 1994; Grant and Brown 1998a). In contrast, *Gadus ogac* settle in a single recruitment pulse in July-August (Laurel et al. In press, Chapter 2).

Mark-recapture experiment:

A mark-recapture experiment was performed between August 16 - September 3 in 1999 on the western shore of inner Newman Sound in Terra Nova National Park (48

35'N, 53 55'W). Fifteen adjacent seine sites (16m wide) were marked with flagging tape along 274 m of unobstructed shoreline (Fig. 2); the survey area encompassed 13 504 m^2.

We collected 1109 *Gadus* spp. (47% *G. morhua*; 53% *G. ogac*) on August 18 from site 4 (i.e. location 0 m) and mass-marked with fluorescent grit following the procedure described by Phinney et al. (1967). The marking apparatus consisted of a marking gun (commercial sandblast gun) retrofitted with a 5 mm orifice and attached canister holding Saturn Yellow™ fluorescent grit (DayGLO Color Corp.). The marking apparatus was attached to a scuba cylinder with a high-pressure hose and regulator that reduced air pressure to 550 kPa during marking. Fish (50-250 at a time) were marked in a plastic tub (W: 0.5m, H:0.5m, L 1.0 m) with a screen bottom (1 mm mesh). The plastic tub was nested in a similar sized tub holding ambient seawater to minimize the time fish spent out of water. The marking gun was held *c.* 40 cm from the fish and sprayed for 2-3 seconds. Fish were then transferred to partially submerged, plastic holding pens at the site of capture. Marked individual were released back into the site of capture (Site 4; Fig. 2) ten hours following the last batch marking.

A recapture seining series was initiated on day 1 (15 hrs after release) and repeated on days 2, 6, 9, and 16. Two seining teams sampled simultaneously in opposite directions starting from sites 5 and 6 and worked outwards towards sites 1 and 10 respectively. Captured juvenile cod were transferred to holding containers with seawater and examined under ultraviolet light in a dark tent for presence of fluorescent marks. All fish were transferred to holding containers and released after seining was completed for the day, after which fish were released back into the site of their recapture.

Laboratory experiments:

Fish collection

Juvenile age 0 *Gadus morhua* (70-90 mm SL) were caught by beach seine (See Laurel et al. 2003 for seine description) from additional sites elsewhere in Newman Sound and transferred to the laboratory. Fish were held in 1 x 1 x 0.5 m flow-though tanks at ambient water temperature and fed a mixture of chopped herring and commercial pelleted food. Fish were allowed to acclimate to laboratory conditions for a period of two-weeks prior to initiating experiments.

Experimental design

Juvenile cod distribution was digitally videotaped over sand and simulated eelgrass in a large flow through tank (2.0 x 1.5 x 0.4 m) maintained at 5-10° C. A digital video camera, fixed with a wide-angle lens, was mounted 2.2 m directly above the tank. The field of view and focus of the camera were locked to maintain a clear, perpendicular view of the entire tank and its inhabitants. The camera could be operated remotely from an adjacent room outfitted with a video-screen to start and stop trials. Illumination was provided by two 1.8 m high light stands on opposite sides of the tank; each light stand was fitted with two 300-W halogen lamps. Lamps were angled at 45° into each side of the tank to highlight fish as well as intentionally create a shadow on the tank bottom.

Bottom habitat was switched repeatedly between trials to either unvegetated sand or simulated eelgrass. Sand (< 1 mm) was washed and placed into the tank to cover the entire bottom at a thickness of 10 cm. Eelgrass was manufactured by attaching green, plastic ribbon (W: 0.8 cm H: 20 cm) to mats of galvanized wire fencing at a density of

400 blades m^2. During placement of eelgrass into the tank, fencing was fully covered by a sand layer so that only the ribbon was visible during trials as the. Simulated eelgrass emerging from the substrate varied in length between 17-19 cm. Field experiments have shown that similarly constructed eelgrass attracts (Laurel et al. In press, Chapter 2) and reduces predation of juvenile cod (Laurel et al. 2003, Chapter 4).

Five experimentally naïve age 0 juvenile cod (*Gadus morhua*; 7.8 ± 0.14 cm) were transferred from holding tanks to the experimental tank using a 2 L transparent glass container with ambient seawater. Fish were allowed to acclimate to the temperature of the experimental tank by placing the holding container in the center of the tank for 15 min. Fish were then released into the tank and filmed for a 1-hr period. All operations to manipulate the camera were conducted in a separate room to minimize disturbances during a trial. Following each trial, fish were collected by dip net and moved to a separate holding tank. A total of ten 1-hr trials in each habitat (eelgrass and sand) were recorded over 3 weeks.

Video analysis

Digital video recordings were uploaded to a computer with image analysis software (Matrox Inspector™) to gather 3-dimensional positioning and orientation data for each juvenile cod. Frame grabs of video were insufficient by themselves because fish were difficult to distinguish against the heterogeneity of the habitat. Instead, short 10-s clips of video were captured and looped repeatedly from a reference frame. Fish were digitally marked at the reference frame while the video looped to reveal the position of

each fish. Reference frames along with 10-s video clips were captured at 3-min intervals for 57 minutes during each trial (n=20 reference frames/trial).

From each reference frame I gathered the orientation and position in space (x,y,z coordinates) of each fish. Orientation was acquired by drawing a digital line from head to tail of each fish from each reference frame (n=5 angles/frame, 100 angles/trial). The software outputs an angle (0-360°) based on the counterclockwise difference between digitally marked fish and a 3 o'clock reference line. To calculate fish position, a digital point was placed at the anterior end of each cod in each reference frame (n=5 x,y-coordinates/frame, 100 x,y coordinates/trial). From each digital point, the Cartesian coordinate system of the software outputs a fish position in a 2-dimensional plane (x,y) to the nearest 0.5 centimeter. The 3rd dimension (i.e., fish height in the water column) was calculated from the distance of its x,y position to its cast shadow on the substrate. Because the distance of the cast shadow is dependent on the position of the fish in the tank, shadow distances were corrected based on the shadow mapping algorithms outlined by Laurel et al. (submitted, Chapter 5). In rare instances when the walls of the tank obstructed the shadow cast when a fish was adjacent to the tanks walls, the last known shadow-body distance for that fish was used.

Data Analysis:

Field seines:

Juvenile cod densities estimated from seines catches were examined using quantile-quantile plots of % abundance versus % area to determine the degree of aggregation of fish in the field i.e., Lorenz curves (Dagum 1985). Plots were constructed for eelgrass and sand separately for each year by first calculating the percentage of the

total population within a year associated with a single seine haul i from either eelgrass or sand sites:

$$1) \qquad n_i = 100(w_i + 1) / \bar{E}$$

where w_i = number of fish caught in a seine haul and $\bar{E}$ = mean catch per haul. These data were compared against the percentage area associated with each tow ($A_i = 100\ c_i$) where c_i was the proportion of the annual catch in a single seine haul i. I sorted seine hauls by n_i and plotted cumulative percent area against cumulative percent abundance for each year, species and habitat. A highly concave curve shows high aggregation whereas increased linearity with a slope approaching 1 indicates an even distribution of fish among seine hauls. The range in concavity is loosely related to the statistical distribution (e.g., normal, poisson, negative binomial.) of the catch data (Fig. 3). The total area underneath each curve (k) was integrated ($\int k$) to determine the discrepancy from a perfectly even distribution i.e., 1:1 line. $\int k$ was then plotted against the corresponding yearly mean catch to determine if density was related to aggregation as measured by $\int k$. Data were then log transformed and regressed to determine if $\int k$ increased with annual abundance. Such a relationship would indicate a density-dependent effect on aggregation.

We also examined within-site aggregation over the course of a season (July-November). Within-site catch variability for each year and each species was determined using coefficients of variation (CV) of bi-weekly catch data ($w_i + 1$). These data were regressed against the log transformed total catch within each site for each species within a

year (LOG (W_{tot} +N_{tot})). Residuals from regression met the assumptions of normality and homogeneity.

Mark-recapture:

Movement rate was calculated by regressing the number of recaptures against time:

$$2) \qquad \ln (N+1) = \alpha + \beta (T)$$

where N was the number of recaptures of juvenile cod and T was the time in days. A constant (N+1) was added to the equation to include possible days when 0 fish would be recaptured. I determined movement rate from the slope (100*β) and expressed it as % fish day^{-1} leaving the survey area.

Video data:

I determined the degree of aggregation in tank trials by calculating distances between all fish in each reference frame. The distances between one fish in space (*Ax, Ay, Az*) and a second fish (*Bx, By, Bz*) was calculated using the following equation:

$$3) \qquad Dist_i = \sqrt{(dx^2 + dy^2 + dz^2)}$$

where *dx=Ax-Bx*, *dy = Ay-By* and *dz = Az-Bz*. The total sum of all possible distances between fish in each reference frame (n= 10 distances/frame) was then used to calculate an aggregation coefficient (n=1/frame, 20/trial). I used one-way ANOVA with repeated measures to determine if mean aggregation coefficients within each trial (n=10 eelgrass, 10 sand) differed between habitats. Habitat (eelgrass or sand) formed the between group

factors in the model. Time (min) of observation (e.g.,0, 3, 6, 9 ...57) within the trial was examined as a within group factor.

We determined how groups of fish oriented over different habitats (n=10 angle differences/ frame, 200 angle difference/ trial) by examining the similarity between angles within a reference frame. The minimal sum of the angle difference (A_D) between each fish and its neighbors for each reference frame was calculated using the following equation:

$$4) \qquad A_D = \min \left| \sum_{i=1}^{n} Ang_i - Ang_{i+1} \right|$$

where Ang_i is the orientation (in degrees) of a single fish relative to a 3 o'clock position. Angle differences were transformed so that $Ang_i - Ang_{i+1} < 180$. If $Ang_i - Ang_{i+1} > 180$, angles were adjusted using the equation:

5) $360 - [Ang_i - Ang_{i+1}]$.

I used the minimal sum, which consisted of one reference fish relative to its four other neighbors (n=5 angle difference/sum), as the test statistic from which to measure group orientation. Lower sum values indicated that fish were oriented in the same direction whereas high sums suggested that fish were moving in separate directions. Mean minimal angle sums (n=20/trial) were compared between habitat treatments using one-way ANOVA with repeated measures (n=10 eelgrass, 10 sand). The assumptions for computing p-values were checked by examining residuals for normality and homogeneity. Habitat (eelgrass or sand) formed the between group factors in the model and time (min) of observation within the trial was examined as a within group factor.

RESULTS:

Field catch data:

There was a significant high interannual variability in late summer and autumnal catches of both *G. ogac* and *G. morhua* (Fig. 4). This was most pronounced in *G. morhua* with more than an order of magnitude difference in mean catch, ranging from a high catch in 1999 (87.3±22.3 fish haul^{-1};mean±se) to a low catch in 2001 (4.6±0.9 fish haul^{-1}). In contrast, *G. ogac* ranged from a high catch in 1999 (118.5±56.9 fish haul^{-1}) to a low catch in 1996 (19.1±7.0 fish haul^{-1}).

Both *G. o*gac and *G. morhua* aggregated more in sand habitats than eelgrass habitats in most years (Fig. 5), but the degree of aggregation was highly variable in sand habitats between years for both species. The interannual variability in the degree of *G. morhua* aggregations over sand was significantly related to interannual fluctuations in density (n=5, r^2=0.93, p = 0.004; Fig 6). However, no relationship was found for *G. morhua* in eelgrass sites (n=5, r^2=0.11, p=0.636) or for *G. ogac* in either sand (n=5, r^2=0.28, p=0.103) or eelgrass (n=5, r^2=0.01, p=0.979). Therefore, only *G. morhua* became more aggregated over sand habitats when abundance in eelgrass habitats was higher.

Within-site temporal variability was correlated with abundance in sand for both *G. ogac* (n=17, r^2=0.83, p<0.001) and *G. morhua* (n=17, r^2=0.79, p<0.001) but not in eelgrass (*G. ogac* n=39, r^2=0.01, p=0.829; *G. morhua* n=39, r^2=0.02, p=0.444; Fig. 7). These data suggest that, for both cod species, high abundance within a sand site is due to a few large aggregations of fish. In contrast, individual eelgrass sites were much less variable at high abundance, indicating consistent catches over time in this habitat.

Mark-recapture experiment:

There was significant negative relationship (r^2=0.84, p=0.0181) of daily recapture of juvenile cod (*Gadus* spp.) with time (Fig. 8a). Fewer fish were caught on day 6 as a possible result of sampling during heavy rainfall, causing fish to move into deeper water to avoid contact with freshwater run-off. I interpret these trends as cod movement rather than mortality since marked individuals were caught progressively further from the area of release on successive days (Fig 8b.). Sixty-three percent of fish recaptured were caught at either the original site of release or within the two adjacent sites. The remaining 27% of recaptured juvenile cod strayed from the release site to occupy fringing sites in the survey area. From the regression equation:

$$\ln (N+1) = 2.70 - 0.167*T$$

we calculated the mixed-species movement rate of juvenile cod as 16.7% d^{-1} from an area of 13 035m^2 (237 m x 55 m).

Video trials:

Video analysis indicated that juvenile cod were more aggregated over sand habitat than eelgrass habitat (ANOVA with repeated measures, $F_{1,18}$=21.716, p<0.001; Fig 9). Within-subject analysis indicated a measurable effect of aggregation over time in sand ($F_{19,179}$=4.165, p=0.028) or eelgrass ($F_{19,179}$=8.025, p=0.011). Fish were highly aggregated in both habitats early in the trial as a result of being released from a common starting position in the tank. Increases in juvenile cod dispersal in both eelgrass and sand appeared to level off after 20 minutes into the trial, but fish in eelgrass treatments were

clearly more dispersed at this point (Fig. 9). No aggressive behaviour was noted between individuals in either treatment.

There was weak evidence that propensity to swim in parallel differs between habitats. Fish over sand habitat were oriented in a common direction more so than fish in eelgrass habitat. However, the analysis showed this to be just outside the statistical alpha (ANOVA with repeated measures; $F_{1,18}$=3.36, p =0.087; Fig. 10). Within-subject analysis also indicated no measurable change in orientation over time in sand ($F_{19,179}$=.165, p=0.828) or eelgrass ($F_{19,179}$=.122, p=0.751).

DISCUSSION:

The relation of juvenile cod and habitat have been explored from field observations (e.g. Tupper and Boutilier 1995a,b, Gotceitas et al. 1997), lab experiments (Gotceitas et al. 1995, Fraser et al. 1996, Lindholm et al. 1999) and field experiments Linehan et al. 2001, Laurel et al. 2003, Laurel et al. In press, Chapter 2, 4). However, this study provides the first evidence that observed variation in catch of age 0 juvenile cod is the result of habitat-induced changes in aggregative behaviour e.g., shoaling or schooling. Juvenile cod use of low complexity habitats (i.e., sand) was ephemeral and aggregative in nature. More significantly, however, these aggregation patterns for *G. morhua* were magnified over sites with low habitat complexity in high abundance years. Therefore, my study provides a clear example of a density-dependent, habitat-related change in behaviour of a marine fish. Consequently, habitat suitability for Atlantic cod should be considered as a dynamic rather than static function if aggregative behaviour modifies fitness in these habitats.

The effects of space limitation have been widely explored in marine fish. Organisms may use poorer quality habitat (e.g., low food, high risk) when high quality habitat (e.g., high food, low risk) becomes saturated (e.g., McCall 1990; Kramer et al. 1997). Fish settling in poor quality habitat may either die (e.g., Connell and Jones 1991; Tupper and Boutilier 1995a) or face poor growth (Sogard 1992). My data from field sampling, mark-recapture and video observations all demonstrate that fish settling in poor habitat can also switch to another behaviour. This "behaviour switching" hypothesis is supported in several lines of evidence. First, *G. morhua* and *G. ogac* were caught in sand habitats infrequently, and when present, they generally occurred at high densities. Second, video observations confirmed that *G. morhua* aggregated more over sand. Finally, mark-recapture data demonstrated that both cod species move extensively following settlement. I suggest that this aggregation behaviour in open habitats either reduced predator risk or was possibly in response to the unique foraging opportunities available there (Savino and Stein 1982; Pitcher 1986).

Living in groups has a number of antipredator and foraging advantages. Increased shoal cohesion has been shown to occur in fish when exposed to increased predation risk (Andorfer 1980; Magurran and Pitcher 1987). Possible anti-predator benefits include increased predator detection (Bertram 1978), confusion (Milinski 1979; 1985) and dilution (Foster and Treherne 1981; Krebs and Davies 1991 but see Pitcher 1986 for alternative view). These mechanisms may offset the cost of increased conspicuousness of group living and ultimately reduce predation rates for species living in groups (Calvert et al.1979, Foster and Treherne 1981), including fish (e.g., Neill and Cullen 1974, Tremblay and Fitzgerald 1979). Foraging benefits include increased search

rates and information gathering and sharing (Pitcher et al. 1982). Studies have shown that fish in large groups can allocate more time to foraging in open substrates since less time need be spent refuging in complex habitats (Magurran and Pitcher 1983). However, under certain conditions, habitat specific behaviour can lead to increased mortality. For example, gobies increase their activity levels in open habitats, which ultimately leads to increased predation rates (Tallmark and Evans 1986). It is therefore difficult to speculate on the advantage of juvenile cod shoaling in sand in years of high abundance since I did not measure the fitness consequences of such behaviour. Based on the mixed evidence of benefits stemming from habitat-specific behaviour, it may be that shoaling over poor quality habitat is the result of juvenile cod "making the best of a bad situation" rather than a fitness strategy suitable in all years.

High densities of juvenile cod were found associated with eelgrass in all years, suggesting this is a preferred nursery habitat for these two species. Complex habitats such as eelgrass generally support a higher number of species and density of fish than habitats of low complexity (Orth 1984, Bell and Pollard 1989). Eelgrass often supports higher densities of food, namely in the form of pelagic and epiphytic zooplankton. Macrophytes also reduce the risk of predation for young fish from larger piscivores (e.g., Werner and Gilliam 1984, Mittelbach 1986) including juvenile cod from known predators such as older conspecifics (Bogstad et al. 1994) as well as red hake (*Urophycis tenuis*), sculpin *Myoxocephalus* spp. (Linehan et al. 2001, Laurel et al. 2003, Chapter 4). Juvenile cod have also been shown to use the interstitial spaces of less complex mineral substrates such as cobble and gravel for predator avoidance (e.g., Lough et al. 1989, Gregory and Anderson 1997). However, the substrate particle size at the sand sites was

c. < 1 mm, and therefore, unsuitable for cover. Predation risk is higher over substrates with particle sizes < 4 mm (i.e., sand; Gotceitas and Brown 1993) and consequently, age 0 cod are seldom observed over small particulate substrate either inshore (Laurel et al. In press, Chapter 2) or offshore (Lough et al. 1989).

There are conflicting reports on the range and degree of age 0 juvenile cod movement following settlement. Age 0 juvenile cod have been observed defending areas of habitat in the field (Tupper and Boutilier 1995ab) and the laboratory (Gotceitas and Brown 1993). Tupper and Boutilier (1995ab) also document high site fidelity and limited within-habitat movement for juvenile cod. However, my data stand in contrast to previous discussions of territorial behaviour and limited movement. In both of the above studies, variable use of habitat was attributed to differential, predator-induced mortality between habitats rather than movement. Grant and Brown (1998a) observed some movement in *G. morhua* in nearshore areas of Newfoundland, but they suggest these movements were infrequent and restricted to a few hundred meters. A subsequent study (Grant and Brown 1998b) showed a diel inshore-offshore movement of juvenile cod, possibly in response to temporal changes in prey availability and predator risk.

Mark-recapture data from the present study suggest juvenile cod movements are spatially and temporally greater than previously reported. Differences in reported movement between studies may be linked to unique genetic or phenotypic aspects of the populations studied. Little to no mixing occurs between the Scotian shelf (i.e., area of Tupper and Boutilier's study) and the northeast coast of Newfoundland (our study; Ruzzante et al. 1988). Species of fish can have static and resident components even at small spatial scales (Stott 1967; Taylor 1990; Heggenes et al.1991; Freeman 1995).

Therefore, variable movement within genetically discrete populations should be expected. Moreover, juvenile cod from the two populations grow under differing temperature regimes. Growth of juvenile cod in St. Mary's Bay cod can reach 2.27 mm d^{-1}(Tupper and Boutilier 1994b) relative to *c.* 1.5 mm d^{-1} from cod collected in my study (Gregory and Laurel unpub data). Phenotypic variability (e.g., growth, body size, etc) often corresponds with a change in behaviour, including strategies of feeding (e.g., Lavin and McPhail 1987), predator defense (e.g., Bronmark and Miner 1992), and territoriality (e.g., Taylor 1990). These differing strategies may ultimately contribute to differing patterns of movement in and among habitats. Lastly, movement rates in fish can also be influenced by the degree of habitat heterogeneity. Fish movement may decrease in preferred habitats if those habitats are isolated or surrounded by unfavorable habitat i.e., 'oasis effects' (Virnstein and Curran 1986; Schroeder 1987; Sogard 1989). Grant and Brown (1998) report limited movement of juvenile cod between sites following settlement in nearshore areas suggesting there were large sections of unfavorable habitat between sampling sites. Age 0 juvenile cod are restricted to shallow, nearshore habitat such as eelgrass, possibly due to increased predation with depth (Linehan et al. 2001) and reduced habitat complexity beyond the littoral zone. Mark-recapture studies conducted between areas of varying habitat and depth may therefore misrepresent the capacity of movement in juvenile cod. In my study, juvenile cod movement was measured in an unobstructed eelgrass meadow, possibly explaining the higher rates of movement rates compared to those reported in other studies on juvenile cod.

Although both cod species used habitat similarly within years, interannual differences in habitat use were only linked to density in Atlantic cod. No studies on

density and habitat use have been reported for age 0 *G. ogac*, but differences between the congeners may stem from life-history differences. Atlantic cod spawn both inshore (Hutchings et al. 1994) and offshore (Templeman 1979), have pelagic eggs (Scott and Scott 1989) and often rely on local hydrography (i.e, retention areas) for survival (de Young and Rose 1993, Page et al. 1999, Bradbury et al. 1999). Consequently, Atlantic cod are subject to high variability in interannual abundance. *G. ogac* on the other hand, have demersal eggs and are spawned inshore within nursery areas (Scott and Scott 1989). Demersally spawned eggs are more likely to be retained than pelagic eggs (e.g., Bradbury et al. in press) so interannual variation in recruitment in these species may be less extreme. My results support this interpretation. *G. morhua* abundance ranged 20-fold from a low catch in 2001 to a high catch in 1999. *G. ogac*, on the other hand, were abundant and less variable between years i.e., ~ 6-fold change.

G. morhua expand their range during years of higher abundance (Rose and Leggett 1991, Swain and Wade 1993, Anderson and Gregory 2000). Although I did not measure range expansion directly, it is interesting to note that substantive catches of juvenile cod in sand habitat were restricted to high abundance years. Such an observation is consistent with the density-dependent spillover effect, but inconsistent with a previous study in Newfoundland where no effect of density was found on range contraction in juvenile cod (Schneider et al. 1997). Differences between the observations in my study and the analysis by Schneider et al. (1997) may be an issue of scale. Schneider et al. (1997) analysed catch data over a 1500km range of coastline and therefore results could have been affected by larval supply due to localized spawning success of several populations (Hutchings et al. 1994). For example, sites may never be occupied, even in

years of highest abundance, if local hydrography prevents larvae from settling nearby. Consequently, there is increased probability of Type II error if such sites are included in an analysis on shifts in geographic range due to density. My study was restricted to a bay scale (i.e., < 30 km) and previous work within this bay has shown that differential habitat use patterns by juvenile cod are not the result of larval supply (Laurel et al. In press, Chapter 2). However, it remains to be determined whether the patterns of distribution observed in this study are relevant at larger scales.

CONCLUSION:

Field sampling and lab observations show that juvenile cod aggregate more over unstructured habitats (i.e., unvegetated sand) compared to structured habitats i.e., eelgrass. In every year examined, higher densities of both species of juvenile cod were found in eelgrass, suggesting unvegetated sand is an unfavorable habitat. It is possible that aggregating over sand is a means of offsetting the costs (i.e., high risk and low food) associated with using these habitats. Aggregation of Atlantic cod also increased over sand sites in years when abundance in eelgrass habitats was high, indicating this behaviour is density-dependent. Mark-recapture experiments suggested that juvenile cod are not as site-attached as previously reported, and that aggregations are likely the result of movement in and out of sites rather than mortality over time. Video analysis also demonstrated that juvenile cod form more cohesive shoals over sand, consistent with the interpretation of field catch data. Together, these data underscore the importance of considering density along with behavioural flexibility when evaluating habitat suitability in fish.

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FIGURE CAPTIONS:

Fig. 1: Study area in Newman Sound, Bonavista Bay, Newfoundland showing sand (□) and eelgrass (■) seine locations.

Fig. 2: Illustration of the layout of sites seined to measure movement of *G. ogac* and *G. morhua* on a 219 m section of shoreline in Newman Sound, Bonavista Bay, Newfoundland between August 18-September 3, 1999.

Fig. 3: Quantile-quantile plots for randomly generated data from normal, Poisson and negative binomial distributions (k<1). High concavity suggests high aggregation of an organism in time or space.

Fig. 4: Mean seasonal (July-November) catch of *G. ogac* and *G. morhua* at sand and eelgrass sites from 1996, 1998-2001. Values between 1998-2001 are based on 70-80 seine hauls ± 1 S.E. 1996 values are based on 10-20 seine hauls ± 1 S.E

Fig. 5: Quantile-quantile plots of interannual seine-catches *Gadus morhua* and *Gadus ogac* (1996, 1998-2001). Each curve comprises the seasonal catch (Jul-Nov) of fish in a single year.

Fig. 6: Relationship of yearly aggregation (quantile-quantile plot integration) and yearly abundance of *G. morhua* or *G. ogac* in either sand (□) or eelgrass (■). High values on the y-axis indicate low levels of spatio-temporal aggregation.

Fig. 7: Plots of the coefficients of variation of *Gadus ogac* and *G. morhua* against seasonal abundance at seine sites comprised of either a) sand or b) eelgrass. Plotted values represent the coefficient of variation (CV) calculated from 8-10 seine hauls within a year (1996, 1998-2001) at a single location.

Fig. 8: Recapture data (fish per haul n) of juvenile cod (*Gadus morhua* and *G. ogac*) along a 219 m section of shoreline in Newman Sound over a) time (T) in days ($\ln(n+1) = 2.70 - 0.167*T$) and b) *space.

*Meter 0 in the x-axis represents the point of release of marked individuals. Negative and positive values of distance correspond with one or the other alongshore directions.

Fig. 9: Degree of shoaling (interindividual distance) over time (min) of *Gadus morhua* in experimental tanks with eelgrass (n=10 trials) or sand (n=10 trials). Plotted values represent the cumulative distance of each fish to its neighbor from ten trials ± 1 S.E.

Fig. 10: Degree of orientation (angle separation between individuals) of *Gadus morhua* in experimental tanks outfitted with eelgrass (n=10 trials) or sand (n=10 trials). Low values along the y-axis indicate fish are orienting in the same direction. Plotted values calculated from angle sums of five individuals from ten trials ± 1 S.E.

Fig. 1

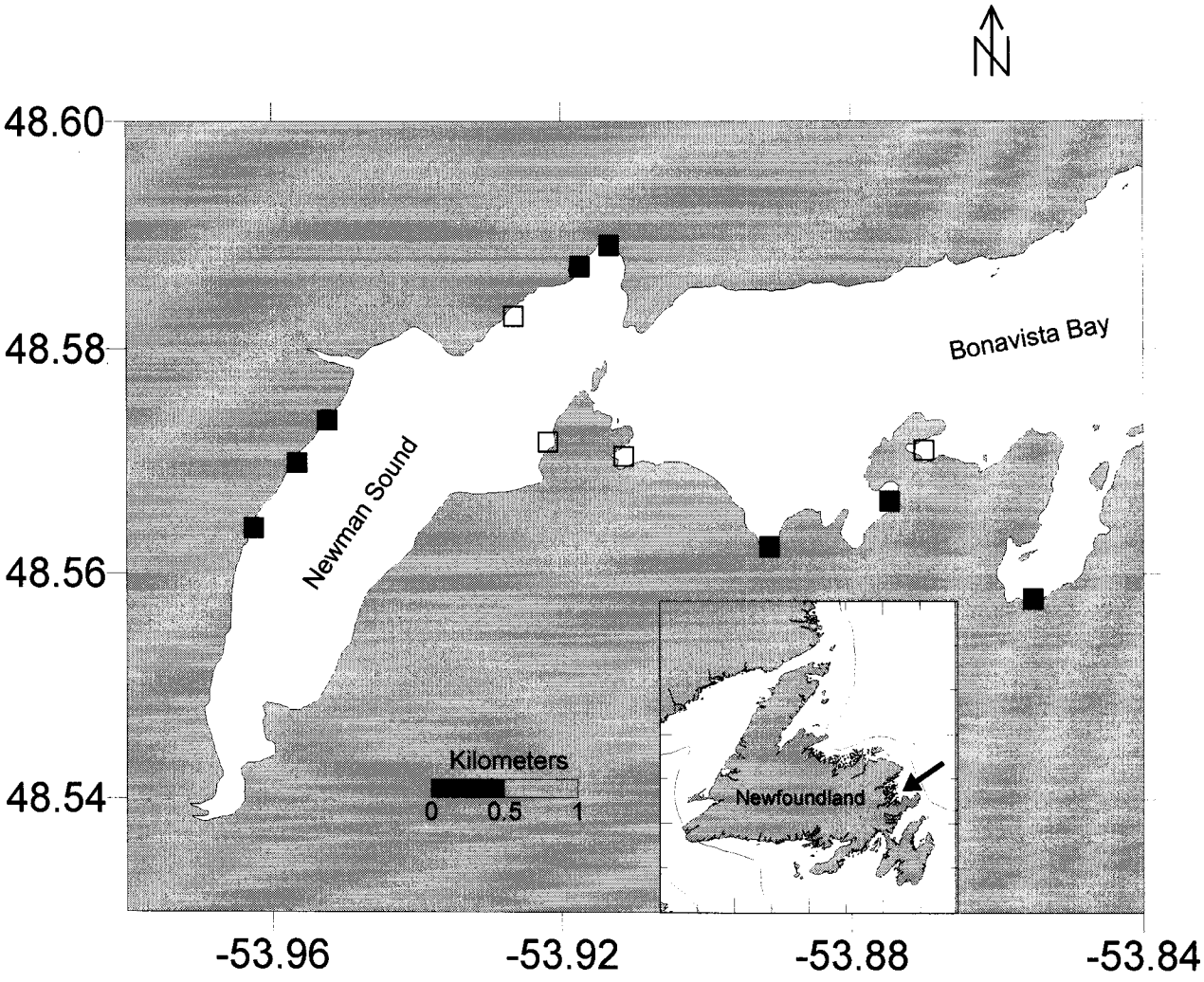

N
48.60
48.58
48.56
48.54
Bonavista Bay
Newman Sound
Kilometers
0 0.5 1
Newfoundland
-53.96
-53.92
-53.88
-53.84

Fig. 2

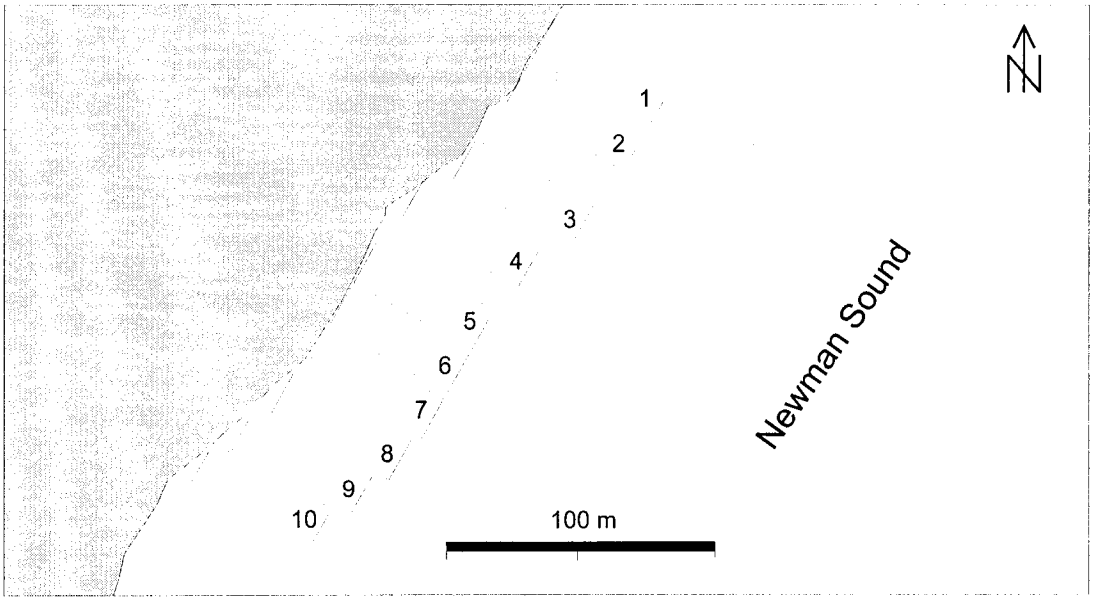


Fig. 3

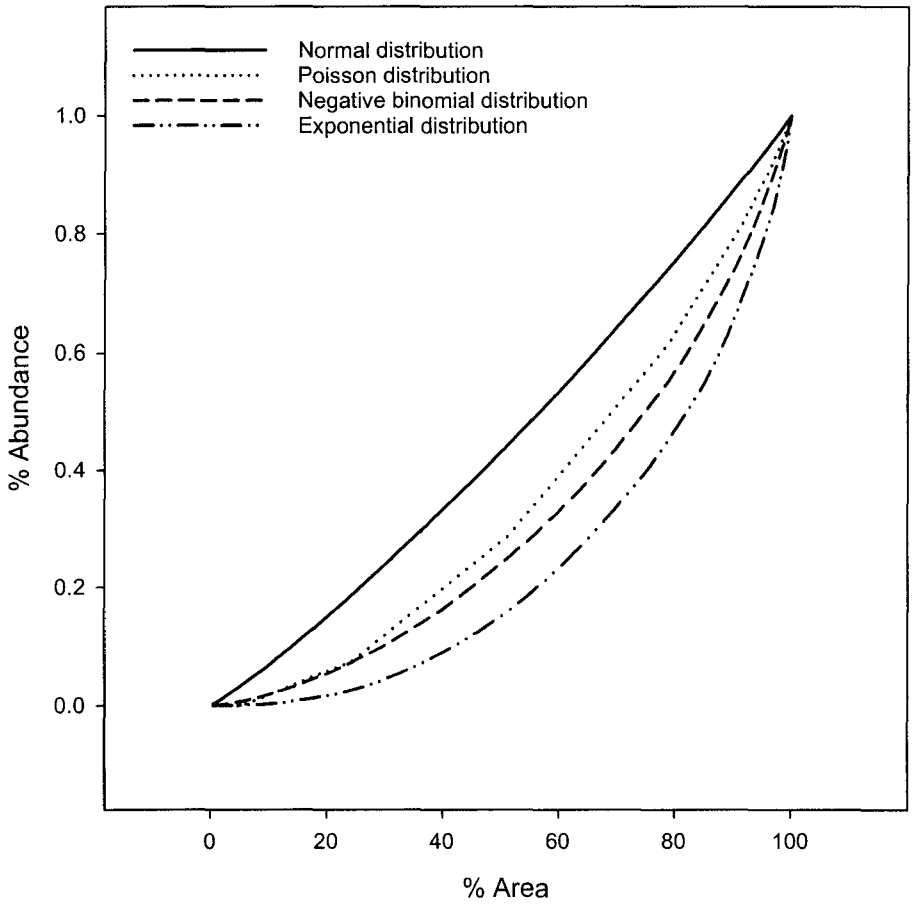

Normal distribution
Poisson distribution
Negative binomial distribution
Exponential distribution
1.0
0.8
0.6
0.4
0.2
0.0
% Abundance
0
20
40
60
80
100
% Area

Fig. 4

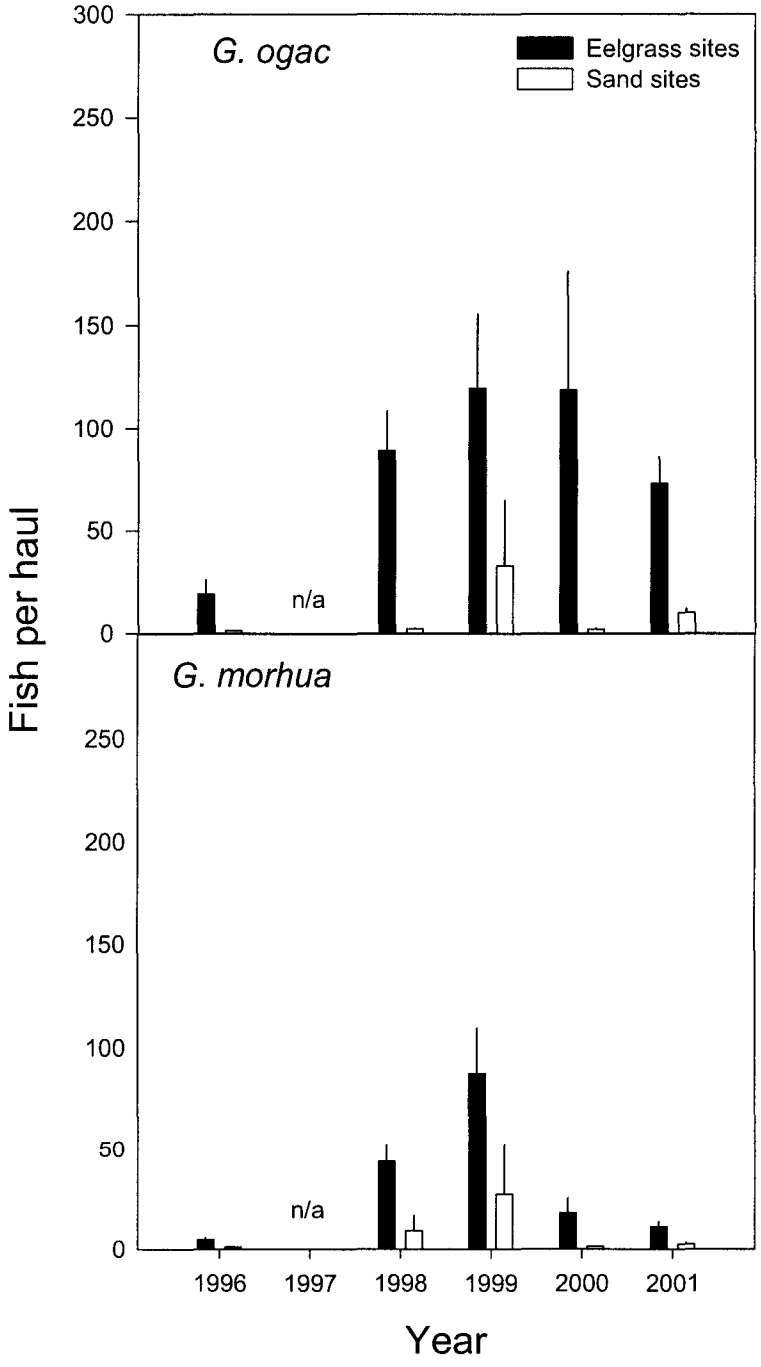

G. ogac
Eelgrass sites
Sand sites
300
250
200
150
100
50
0
n/a
G. morhua
250
200
150
100
50
0
n/a
Fish per haul
1996
1997
1998
1999
2000
2001
Year

Fig. 5

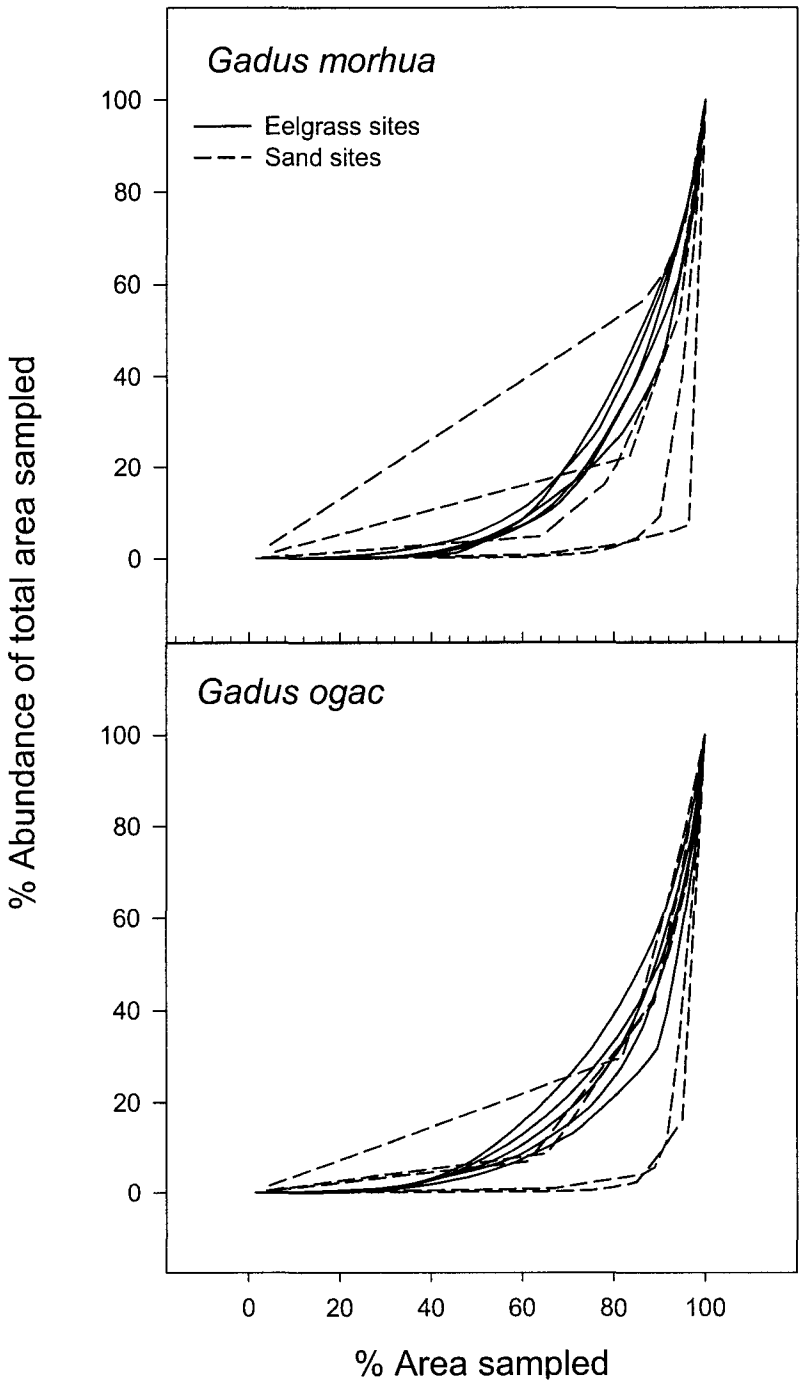

Gadus morhua
Eelgrass sites
Sand sites
Gadus ogac
% Abundance of total area sampled
% Area sampled
0
20
40
60
80
100

Fig. 6

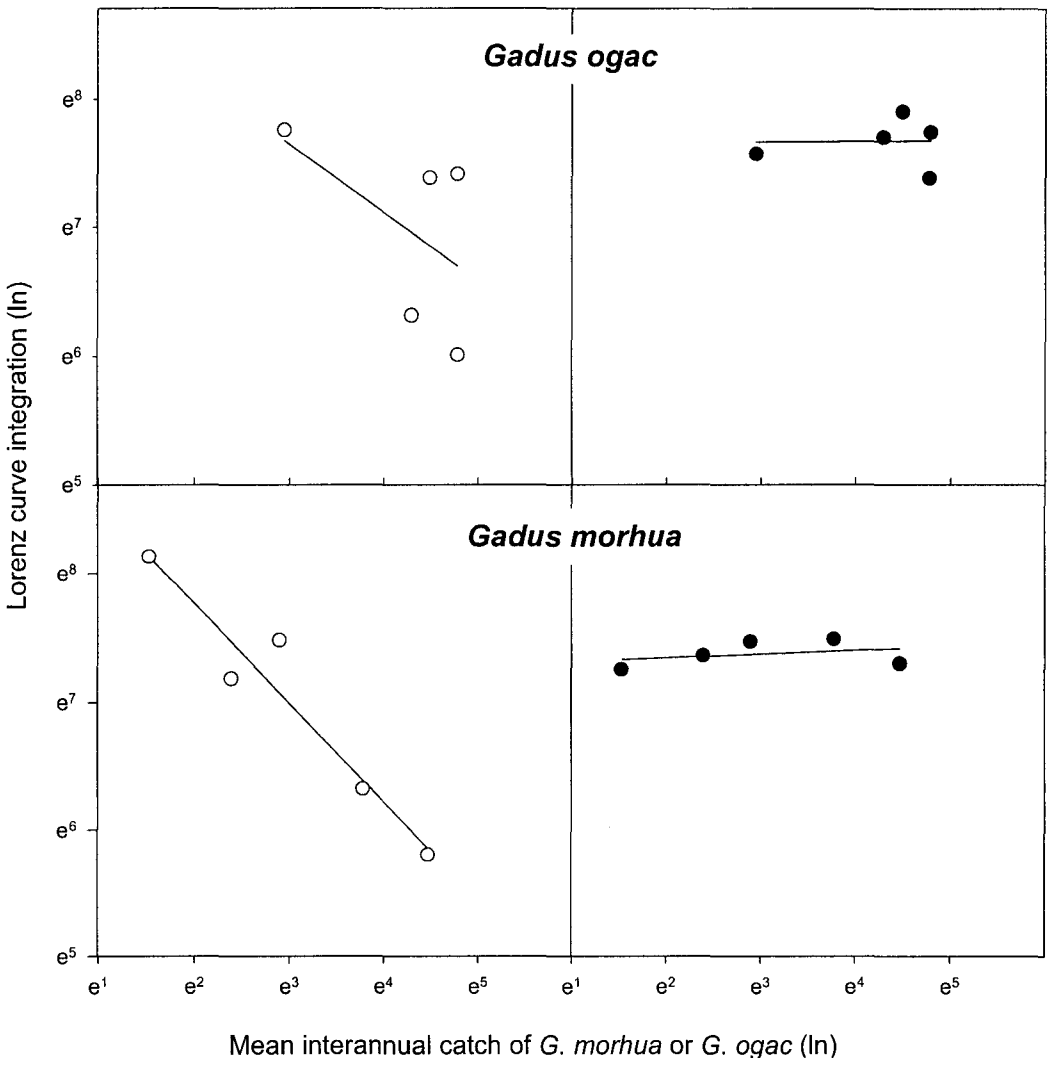

Gadus ogac
Gadus morhua
Lorenz curve integration (ln)
Mean interannual catch of G. morhua or G. ogac (ln)
e8
e7
e6
e5
e1
e2
e3
e4
e5

Fig. 7

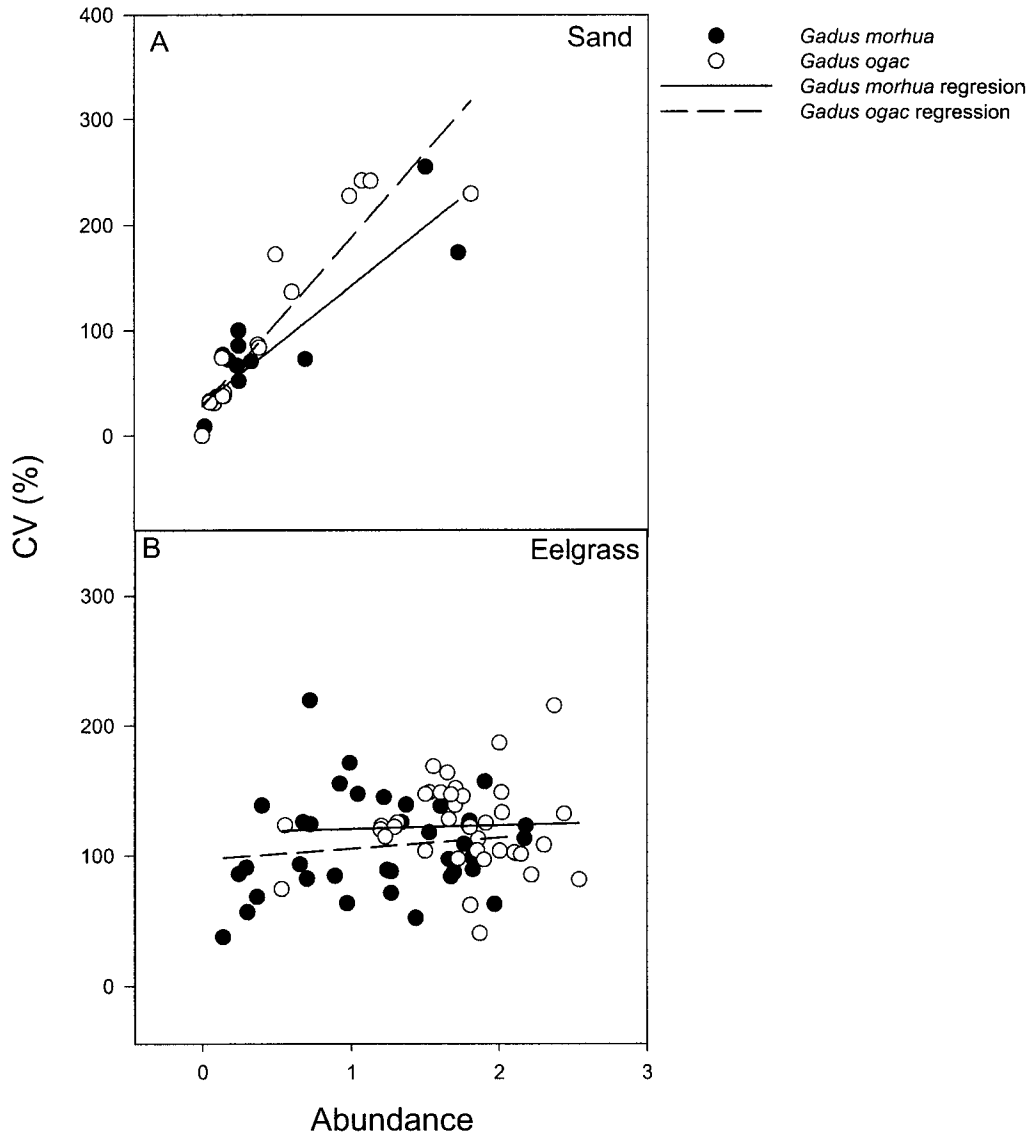

A
Sand
B
Eelgrass
CV (%)
Abundance
400
300
200
100
0
0
1
2
3
Gadus morhua
Gadus ogac
Gadus morhua regresion
Gadus ogac regression

Fig. 8

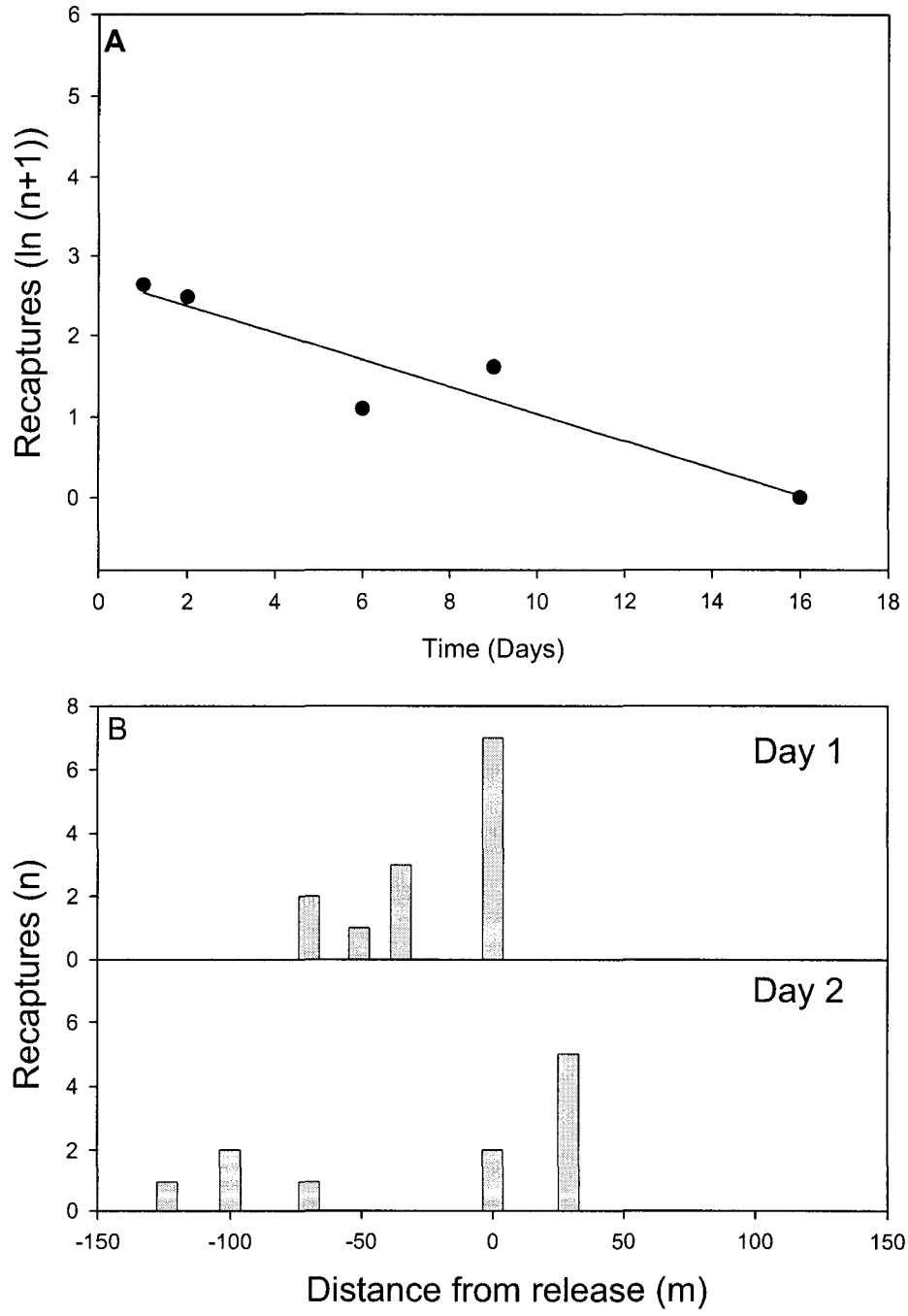

A
Recaptures (ln (n+1))
Time (Days)
B
Day 1
Day 2
Recaptures (n)
Distance from release (m)

Fig. 9

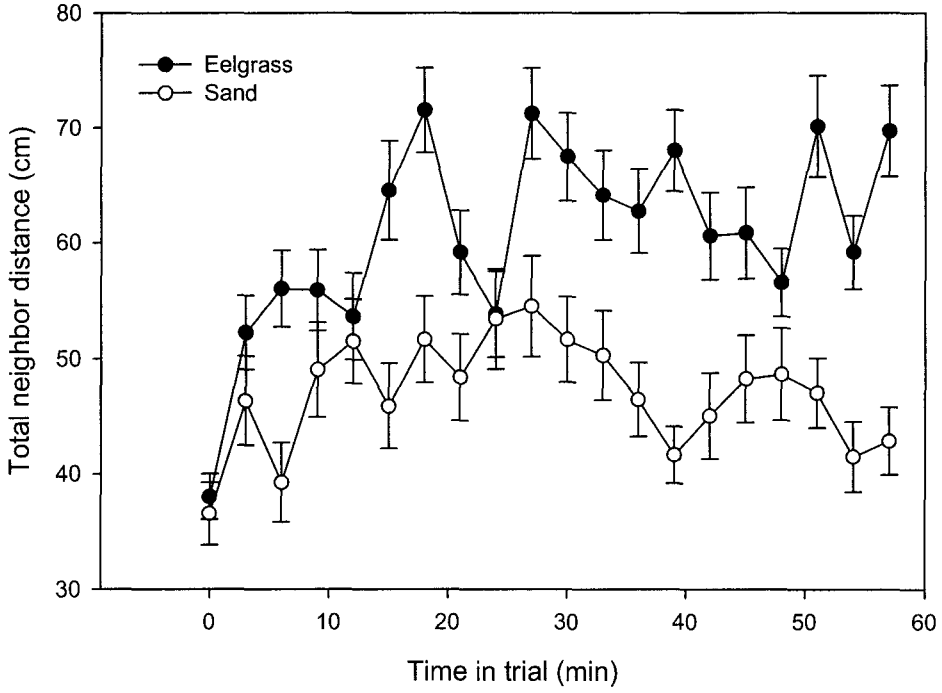
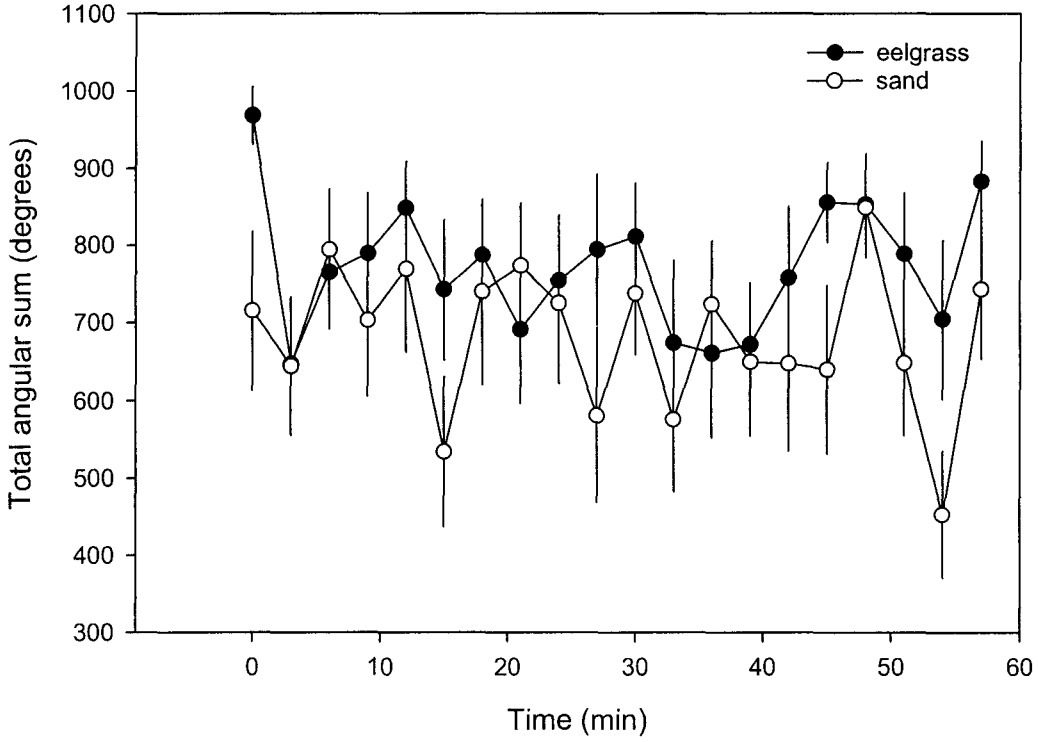

Eelgrass
Sand
Total neighbor distance (cm)
80
70
60
50
40
30
0
10
20
30
40
50
60
Time in trial (min)

Fig. 10


1100
1000
900
800
700
600
500
400
300
Total angular sum (degrees)
0
10
20
30
40
50
60
Time (min)
eelgrass
sand

CHAPTER 4:

Predator distribution and habitat patch area determine predation rates on age 0 juvenile cod (*Gadus* spp).

ABSTRACT:

Eelgrass (*Zostera marina*) provides refuge to numerous fish species but is vulnerable to fragmentation through natural and anthropogenic disturbance. In Bonavista Bay, Newfoundland, eelgrass patch size was altered to measure changes in predation risk in age 0 juvenile cod (*Gadus morhua*). Artificial eelgrass mats of five sizes (0.32, 1.1, 5.5, 11 and 22 m^2) were deployed in duplicate at each of two sites in Newman Sound in Terra Nova National Park during summer-autumn, 1999 and 2000. Predator distribution was determined using a combination of weekly underwater transect surveys and biweekly seining. Relative predation rates were measured by tethering age 0 cod at the center of each patch and recording the incidence of predation (n=1116 tether sets). Predation rates were negatively correlated with patch size during both years, suggesting that larger patches reduce predator foraging ability. However, high predator densities in the largest eelgrass patch resulted in higher than expected rates of predation. Therefore habitat dimension affected predation risk in juvenile cod via two opposing mechanisms. My results emphasize the importance of considering both habitat areal extent and predator distribution when estimating the effects of habitat fragmentation on predation rates.

KEY WORDS: Edge effects · Habitat fragmentation · Atlantic cod · Predator density Tethering · Predator risk

INTRODUCTION:

Seagrass beds provide shelter to a variety of juvenile fish species in coastal environments across a range of latitudes (e.g. Orth et al. 1984, Sogard and Able 1991, Laurel et al. In press, Chapter 2). Fragmentation of these beds occurs both naturally (e.g., seasonal die-off, wave-action and ice scour) and anthropogenically (e.g. inshore boating, nitrogen loading-Fonseca 1992). Consequently, seagrass habitats are often patchy, ranging from single plants to expansive meadows greater than 1000 m^2 (Robbins and Bell 1994).

Juvenile fish often use complex habitats to offset the threat of predation (e.g. Werner et al.1983ab, Mittelbach 1986). However, increased habitat fragmentation of seagrass beds may have negative consequences for young refuge-seeking fish. Predation risk is highest during the early life stages of marine fish (Sogard 1997) and complex habitat reduces risk by interfering with the visual and swimming capabilities of piscivores (Gotceitas and Colgan 1989). However, predators may compensate for reduced foraging efficiency by feeding along the edges of complex habitat (Peterson et al.2001). Therefore, predation risk may be higher in fragmented habitats with increased edge to area ratios (e.g., small patches). Small, fragmented patches may also be riskier because their interior is closer to the more dangerous edges. These explanations have been invoked to explain increasing predation risk with smaller habitat patches in both terrestrial (Levenson 1981) and marine systems (Irlandi 1997).

There has been considerable variation in the results of edge effects/patch size on predation rate (reviewed by Paton 1994). Equivocal results have prompted more studies to examine the local abundance of predators and prey (Donovan et al.1997). For

example, rates of piscivory in eelgrass habitats can be equal to or higher than unstructured sand habitats despite the reduced foraging ability of predators in complex habitats (Linehan et al. 2001; Gregory et al. submitted). Differences in predation rate were attributed to higher numbers of predators in eelgrass habitats compared to unvegetated sand. Therefore, the interactive effects of habitat characteristics (e.g., complexity, perimeter to edge ratios) on predator distribution must be considered when quantifying predation risk across habitats.

Atlantic cod (*Gadus morhua*) is a commercially important demersal species that occupies nearshore areas in the Northwest Atlantic Ocean during their first year of life (Taggart et al. 1994). As juveniles, cod associate with complex habitats such as boulders/large rock (Gregory and Anderson 1997), cobble (Tupper and Boutilier 1995), macroalgae (Keats 1990) and eelgrass (Gotceitas et al. 1997) for protection from predators such as larger conspecifics, piscivorous fish and seabirds. Laboratory experiments have shown that complex habitats can reduce predation risk for juvenile cod when exposed to actively foraging predators (Gotceitas and Brown 1993; Gotceitas et al. 1995; Lindholm et al. 1999). However, recent studies have shown that predators of juvenile cod also prefer complex habitat (Linehan et al. 2001; Wells 2002) and may elevate risk in these habitats. Therefore, the role of habitat characteristics on predation risk in juvenile cod remains unclear.

No studies examining the effects of habitat patch size and local predator abundance on predation rates have been conducted in marine systems. Earlier investigations considering both habitat characteristics and predator distribution have been restricted to a few large-scale avian studies (reviewed by Donovan et al.1997). In this

study, I measured the distribution of piscivorous fish and the rate of predation on tethered age 0 cod in varying sized seagrass patches. I addressed the following questions: 1) Does risk change with increasing eelgrass patch size? 2) How do habitat patch area and localized predator distribution interact to affect risk in age 0 juvenile cod?

MATERIALS AND METHODS:

Study Area:

Newman Sound is located within Bonavista Bay off the northeast coast of Newfoundland in the vicinity of Terra Nova National Park (TNNP; Fig. 1). The nearshore habitat (0-15 m depth) is variable, ranging from eelgrass (*Zostera marina*), macroalgae (e.g. *Laminaria digitata* and *Chondrus crispus*) and fine to coarse grain mineral habitats. I conducted experiments in two coves within the sound: Canning's Cove (CC) and Mt. Stamford Cove (MS). These sites were chosen mainly because they lack any complex habitats such as boulders and/or eelgrass, were of similar depth in the experimental area (1.5-2.5 m) and were also conducive to hauling a net along the bottom.

Artificial Eelgrass:

Artificial eelgrass was manufactured using galvanized screen (2.5 cm pore size) and green curling ribbon (0.8 cm width). Ribbon was tied onto the screen to create blades 75 cm long at a density 400 blades$\cdot m^{-2}$, falling within the range of length and density for naturally occurring eelgrass (Orth et al. 1984). Eelgrass mats were cut into varying length strips to form approximately square patches 0.32, 1.5, 5.5, 11, and 22 m^2 in size. Scuba divers secured replicates of each of these patch sizes to the bottom at each site using reinforcing bar (i.e., re-bar) spikes (Fig 2). Eelgrass mats were attached flush

against the substrate by staggering spikes at 0.5 m distances along their entirety. This reduced possible damage from wave action and also minimized the effect of added complexity from the wire mesh frames. Spacing between patches edges was kept constant at 3 m for both sites. Patches in 1999 were deployed in July, approximately one month prior to age 0 juvenile cod settlement in coastal Newfoundland (Methven and Bajdik 1994; Grant and Brown 1998a). Artificial blades of eelgrass became fouled with epiphytes throughout the season in a similar manner as natural eelgrass. In November 1999, patches were removed, cleaned of epiphytes and stored dry before being redeployed again in July 2000. No significant degradation in the artificial eelgrass (i.e., mesh rust, blade loss, etc.) was observed in either of the two years of the experiment.

Predation Rates:

Predation within patches was determined using a tethering technique with age 0 cod collected by seine from nearby sites. I used two species of cod (58% Atlantic cod *G. morhua* and 42% Greenland cod, *G. ogac*) for tethering. These two species co-occur in the nearshore (Methven et al. 2001) at similar sizes within the first year of life. Susceptibility to predation on tether lines is similar for these two species (B. Laurel and R. Gregory, unpublished data).

The tethering apparatus consisted of two sections, a 2-m 11.2-kg test vertical float line and a 0.5-m 0.9-kg test horizontal leader line. The float line was kept vertical in the water column using a 564 g anchor and a cork float 1 m from the bottom. A white float at the surface marked the location of the tether line and facilitated retrieval. The horizontal leader line was attached to a #7 barrel swivel on the vertical float line 75 cm

from the bottom substrate. Age 0 cod were tethered to the leader line via a #16 hook inserted through the caudal peduncle. The leader line allowed cod prey a 0.5 m radius of movement and access to the eelgrass. A full description of the tethering apparatus and technique is described in Linehan et al. (2001).

Each tether line was deployed from a small aluminum boat (4.2 m) at mid-day, left undisturbed for a period of 15 min and finally retrieved to determine the incidence of predation. Water clarity was adequate to insure that tethered fish were not lost while being lowered to the bottom. Predation was classified as a "hook loss", "fish loss", "caught predator" or "predator attack" upon retrieval of the tether line. The absence of predation was recorded if a tethered fish was retrieved alive without any sign of predation i.e. fully intact without punctured skin. All predators captured on tether lines were identified, measured to the nearest 0.5 cm SL and released.

Our experimental design consisted of setting tethers at the center of each patch (0.32, 1.1, 5.5, 11. and 22 m^2) and on six neighboring areas of unvegetated sand about 3 m from the nearest patch edges. Tethering in patch and unvegetated areas was repeated six times during three tethering sessions in each year ([6 unvegetated areas + (5 artificial eelgrass patches x 2 patch replicates)] x 6 rounds x 2 sites x 3 sessions x 2 years), for a total of 1152 tether sets. Tethering sessions were conducted at *c.* 2-wk intervals beginning early September of both years and corresponded with concurrent surveys of predator abundance. Tethered prey throughout the time period experiment ranged in size from 65-106 mm standard length (SL). The range in size represents growth in the available *Gadus* prey from early September to mid-October of each year. However,

variation in prey size was substantively less within individual tethering sessions i.e. maximum ± 11 mm SL.

Predator Distribution.

Predator abundance was estimated at 2-wk intervals using a 25-m Danish bag seine (19-mm mesh) deployed 55 m offshore from a boat and hauled to shore by two individuals standing 16 m apart. The seine sampled 880 m^2 of bottom habitat up to 2 m in the water column (for description see Methven and Schneider 1998). Captured fish were transferred to holding containers with seawater. Piscivorous fish captured included Greenland cod, Atlantic cod, cunner (*Tautogolabrus adspersus*), sculpin (*Myoxocephalus* spp.), and white hake (*Urophycis tenuis*). Potential predators were identified and measured (± 5 mm SL) and released the same day to their respective sites.

Small-scale, localized predator distribution was measured via snorkeling. Snorkeling surveys were always conducted 3-4 days before or after seining activity to minimize the effects of net disturbance. Snorkelers swam directly over patches, recording the abundance and type of fish predators within 0.5 m of each patch. Large patches (11 m^2 and 22 m^2) exceeded the viewing capability of a single snorkeler, so these patches were assessed by two snorkelers swimming in parallel. Snorkelers swam with delineated poles (2.82 m each) to minimize overlap of survey areas of the large patches. Water clarity throughout the survey was sufficiently greater (i.e., 5-6 m) than the maximum area censused by a single snorkeler i.e. 2.82 m. Experimental sites were visually censused in this fashion between August 10-October 12, 2000 for a total of nine surveys. The survey was not performed in 1999 for logistical reasons.

Additional control snorkeling surveys were conducted at two natural eelgrass meadows of similar depth during the same time period (n=9). Eelgrass at the control sites was continuous (i.e., non-patchy) over the range of the survey area, but only plot areas similar to those at experimental sites were surveyed. This was accomplished by deploying 15-m transect lines perpendicular to shore at each control site. The vertical dimension and spacing of patches was marked on each transect line with pink surveyor's tape while the horizontal dimension of patches was estimated by snorkelers swimming with delineated plastic poles over the transect lines. Snorkelers swam in parallel once over both transect lines at each site so that only areas falling within the delineated transect lines were surveyed ($80m^2$).

Previous studies of juvenile cod indicate that predators greater than 2x the prey size have the potential of capturing and consuming prey items (Bogstad et al. 1994; Grant and Brown 1998b; Linehan et al. 2001). Because of the difficulty in estimating fish size under water, potential predators within patches were size-corrected by integrating seine and snorkel census data using the following equation:

$$P_{tot} = \sum N_{sn} \; l_{se},$$

where P_{tot} is the total potential predators in the patch, N_{sn} is the total predators identified from snorkel surveys and l_{se} is the percentage of predators caught in the seine greater than 2x the mean tethered prey size (mm SL).

Data Analysis:

Tethering data were analyzed using the generalized linear model assuming a binomial error structure on logistically transformed data (log link; proc GENMOD; SAS Release 6.03). 'Year', 'sampling period', 'site' and 'patch size' were used as explanatory

variables. Significant interactions were found between year and site variables, so patches were analyzed separately in 1999 and 2000 within sites. The model assumed a uniform predator distribution; therefore, only patches with similar mean predator density (i.e. ± 2 S.E.) were analyzed. In this way, the effects of habitat structure on predation rates were measured independently of the predator distribution.

RESULTS:

A total of 1152 tethering sets were conducted in both years at two sites. Thirty-six sets were omitted from the analysis because lines were either tangled or fish were dead upon retrieval. The remaining 1116 tether sets were considered successful, of which 12% (138 incidences) resulted in some form of predation. Predation events included "caught predator" (48%), "hook gone" (6%), "fish gone" (22%) and "predator attack" (24%). Predators species retrieved on tether lines included Greenland cod (18.7 ± 3.9 cm SL; $\bar{x} \pm$ sd), Atlantic cod (23.6 ± 4.7 cm SL; $\bar{x} \pm$ sd), cunner (15.8 ± 5.9 cm SL; $\bar{x} \pm$ sd), sculpin (17.0 ± 5.8 cm SL; $\bar{x} \pm$ sd) and hake (12.6 ± 0.5 cm SL; $\bar{x} \pm$ sd). Higher overall predation was observed at MS (16%) than CC (9%).

Predator abundance increased with increasing patch size at both sites as expected (Fig. 3). However, the estimated composition of predators differed between sites as well as by census methods (Fig. 4). For example, cunners were found in greater abundance at CC whereas hake were more numerous at MS. Snorkel and seine surveys indicated that total predator abundance was higher at MS compared to CC. Census discrepancies included Atlantic cod and sculpins. Both were rarely seen over patches during snorkeling surveys but were often caught in seines and on tether lines. In contrast, cunners were often observed in artificial eelgrass patches yet comprised a smaller portion of total seine

catch. However, seine, snorkel and tether data all indicated that *G. ogac* was an abundant predator at both sites (Fig. 4).

Distribution of predators among patches was similar among sites (Fig. 5). At MS, patch sizes 0.3-11m^2 supported similar predator densities (0.037 pred·m^{-2} ±0.006). In contrast, predator density in the largest patch (22 m^2) was 2.3 times higher (0.086 pred·m^{-2} ±0.011) than in the smaller patches. A similar distribution was observed in patches at CC; predators densities in small patch sizes were nearly half (0.030 pred·m^{-2} ± 0.005) of those in the largest patch size (0.059 pred·m^{-2} ±0.08). Therefore, predator density was similar in all patches except the largest (22 m^2) during snorkeling surveys. Differences in 1+ year old Greenland cod abundance were responsible for this trend (Fig. 6). Although, Greenland cod were evenly distributed within natural eelgrass meadows, they were unevenly distributed among artificial eelgrass patches. Cunners and hake did not deviate consistently from expected trends at either eelgrass meadow or patch sites.

Predation rates increased with diminishing patch size at both sites during each year (Table 1; Fig 7) when patches had similar predator density. Data collected from the largest patches (22 m^2) were not included in the analysis because the model assumes uniform predator distribution among patches; only patch sizes 1-4 could meet these assumptions. In 2000, there was a significant effect of sampling date on predation rates at both sites, but no interaction was detected between sampling date and patch (Table 1). Highest predation occurred outside the patches at rates similar to those found over the smallest patches (Fig 7). Lowest predation was observed in the largest patches analyzed i.e.11 m^2.

DISCUSSION:

Structural complexity provides refuge to juvenile fish in freshwater (e.g. Crowder and Cooper 1982, Savino and Stein 1982, Werner et al. 1983ab, Gotceitas and Colgan 1989) and marine (e.g., Sale 1991) systems over a wide range of latitudes (Heck and Wilson 1987). Numerous studies have shown that juvenile Atlantic cod use complex habitats to reduce predation (e.g. Gotceitas and Brown 1993; Gotceitas et al.1995; Gotceitas et al.1997; Gregory and Anderson 1997; Lindholm et al.1999; Linehan et al. 2001). Structurally complex habitats impair the visual and swimming capabilities of predators (Savino and Stein 1982) which in turn can reduce the effectiveness of encountering, attacking and capturing prey (Tallmark and Evans 1986). My results were consistent with these findings. Predation rates of juvenile cod were highest over areas without structural complexity i.e. unvegetated sand. However, I also show that the areal extent of surrounding refuge habitat, along with predator density, also influence the predation risk of small fish.

Age 0 juvenile cod were subjected to highest predation risk in smallest patches when predator density was uniform across all patch sizes. Fragmented habitat patches are considered risky because: 1) they have high perimeter to area ratios and 2) the interior habitat is close to the edge and therefore, accessible to hunting piscivores. While these mechanisms have been explored in terrestrial systems (Brittingham and Temple 1983; Andren et al.1985; Andren 1992; Donovan et al.1997), marine examples have been restricted to a number of invertebrate species (Irlandi 1997; Bologna and Heck 1999; Peterson et al. 2001). My results show that predation risk increases for fish in fragmented environments. The analysis controlled for differential predator density,

suggesting that the patch characteristics are directly responsible for the trend observed. I believe that risk was higher in small patches because of the associated changes in a predator's foraging ability, and not simply predator abundance.

Predator density was not uniform among all habitat patches. The largest seagrass patches (22 m^2) attracted higher densities of piscivorous fish. Consequently, predation risk was higher in these patches than could have been predicted from habitat characteristics alone i.e. patch size. Predator density and predation rates are positively correlated in studies of juvenile cod (Linehan et al. 2001; Gregory et al. submitted). However, the non-linear relationship of predator density with habitat area observed in the present study was unexpected. The higher predator densities in the large patches were due to increased abundance of age 1 + Greenland cod, a species common in nearshore areas around Newfoundland (Methven et al. 2001) and a known predator of age 0 cod (Linehan et al. 2001). The distribution of Greenland cod at the control sites (eelgrass meadows) was linear, indicating that this result was not due to overall patch layout, small changes in depth, distance from shore or area surveyed. Rather, it appears that changes in Greenland cod density were a function of eelgrass patch size.

Nonlinear associations between habitat and organisms are not unique to my study, but the causal mechanisms are uncertain. Species-area curves typically increase with patch size (MacArthur and Wilson 1967) and density for some species has been related to habitat area. For example, European jays (*Garrulus glandarius* L.) and ravens *(Corvus corax* L.) are commonly found in large wooded areas, yet are entirely absent from smaller forest fragments (Andren 1992). Similar findings have been reported for other bird species (Stoufer and Bierregaard 1995) and many species of invertebrates (Kareiva 1985;

Margules et al. 1994; Ingham and Samways 1996; Golden and Crist 1999), including infaunal macroinvertebrate assemblages in eelgrass (Bowden et al. 2001). Small, fragmented patches may not have suitable food or niche space (Galli et al.1976; Martin 1981) or refuge characteristics (Martin 1988) that large patches offer. Eelgrass is known to both concentrate prey (Connolly 1997) and provide shelter to piscivorous fish from predators (Orth et al. 1984). Therefore, predatory Greenland cod may use large patches of eelgrass to balance feeding success with their risk of being eaten. My results suggest that predation risk changes with patch size for small cod (<10 cm), but whether such an explanation applies to the distribution of larger fish (e.g., Greenland cod) is unknown.

I detected no interaction between date and patch size (Table 1), suggesting that trends in predator distribution and risk were maintained within the temporal scale of the study. However, diel, monthly, seasonal and annual changes in piscivorous predators are variable in nearshore areas around Newfoundland (Clark and Green 1990; Linehan et al. 2001; Methven et al. 2001). Therefore, observed trends of predator distribution in my study may not exist at finer (e.g., diel) or broader (e.g., seasonal) temporal scales. Furthermore, such trends will not necessarily result in predictable changes in predation risk for juvenile cod. For example, Linehan et al.(2001) demonstrated a decrease in predation risk at night on age 0 juvenile cod despite increased density of larger conspecifics. Similarly, seasonal differences in temperature can affect the metabolic demands of piscivorous fish and, consequently, risk to their prey species. Overwintering predation in many aquatic systems is therefore considered negligible (e.g. Keast 1978). I restricted my study to August-October, a time of year when juvenile cod predation risk is

high (Linehan et al. 2001; Gregory et al. submitted) and effects of predator distribution on the risk of juvenile cod to predation would be highest.

Inconsistencies in predator density estimates between the seine, snorkeling and tethering techniques are likely methodological artifacts. I suspect that seining more accurately samples predators than visual census. Previous work has demonstrated that demersal fish are caught by the seine technique with 95% efficiency (Gotceitas et al.1997) whereas visual methods can underestimate density due to diver avoidance and fish crypsis (Keats 1990). I estimated density within individual eelgrass patches visually because the seine was not suited to sampling at small spatial scales (*c.* 1-25m^2). The visual census more closely matched seine estimates for site-attached piscivores (e.g., Greenland cod, hake, cunners) that remained associated with eelgrass patches when approached. However, some fish did not associate with patches at these small scales. For example, I routinely observed age 1+ Atlantic cod within close proximity to patches, but I did not include these fish in the abundance estimates as they were "outside" the patch area. Consequently, Atlantic cod were underestimated in snorkel surveys relative to seine catches. Some piscivores may have also been underestimated by the tethering technique due to differential foraging capabilities. For example, cunners were rarely caught on tether lines at either site, yet they were relatively abundant in the areas. Cunners are considered to be omnivorous, feeding preferentially on mollusks and amphipods rather than fish (Scott and Scott 1988). Prey selection is known to be gape-limited (e.g. Schmitt and Holbrook 1984), and cunners, with their small mouths, may have been restricted in their ability to handle the tethered prey in an equal manner to other similar-sized

predators e.g. Greenland cod or sculpins. However, I have observed *in situ* foraging attempts of large cunners (*c.* 25 cm+) on age 0 cod in Newman Sound.

There are limitations of the tethering technique as a means of measuring predation risk in the field. Tethering studies are numerous, including a wide variety of marine and freshwater organism such as decapod crustacea (Heck and Wilson 1987; Wilson et al. 1990; Eggleston et al. 1990), bivalves (e.g. Arsenault and Himmelman 1996), freshwater fish (Gregory and Levings 1998; Post et al. 1998) and marine fish (Curran and Able 1998; Linehan et al. 2001). The technique has its detractors (e.g., Halpin 2000; Kneib and Scheele 2000; Peterson and Black 1994) who have suggested that artifacts confound estimates of predation risk. As a technique to measure relative predation risk between similar habitats, such artifacts are unlikely to confound my interpretations (see Linehan et al. 2001).

In summary, my study is the first to measure the effects of habitat patch size on predation rates in a marine fish species. Eelgrass afforded greater protection to juvenile cod than unvegetated habitat, but both habitat patch size and predator distribution also contributed to differential rates of predation. Small eelgrass patches were riskier to juvenile cod than large patches when predators were evenly distributed, but risk often increased in large patches due to higher predator densities. These results stress the importance of considering both habitat patch dimension as well as predator distribution and abundance when evaluating habitat quality for small fish.

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FIGURE CAPTIONS:

Fig. 1; Study area in Newman Sound, Bonavista Bay, Newfoundland showing the locations of artificial eelgrass patches (■; CC-Canning's Cove and MS-Mt. Stamford) and natural eelgrass locations (□; WR-White Rock and MC-Mistaken Cove).

Fig. 2; Experimental layout of artificial eelgrass patches relative to shore at Canning's Cove -CC and Mt. Stamford-MS (modified from Laurel et al. In press). Tethers set at the center of each patch and six locations outside of patches (indicated by an 'X').

Fig. 3; Mean abundance of predators (*Gadus ogac*, *Gadus morhua*, *Tautogolabrus adspersus*, *Myoxocephalus* spp. and *Urophycis tenuis*) censused via snorkeling at Canning's Cove (CC) and Mt. Stamford (MS) on various sized patches of simulated eelgrass. Each point represents a mean of 9 snorkel surveys of two replicate patches ± 1 SE.

Fig. 4; Proportion of age 0 cod predators (Greenland cod *Gadus ogac,* Gc; Atlantic cod *Gadus morhua,* Ac*;* Cunners *Tautogolabrus adspersus*, Cu; Sculpin *Myoxocephalus* spp, Sc; and white hake *Urophycis tenuis,* Wh) determined by snorkeling, seining and tethering at Canning's Cove (CC) and Mt. Stamford (MS) in 2000. Proportions are based on four beach seine hauls, 288 tether sets and 9 snorkel surveys per site.

Fig.5; Total density of piscivorous predators (Greenland cod *Gadus ogac*, Atlantic cod *Gadus morhua*, cunners *Tautogolabrus adspersus*, *Myoxocephalus* spp. and white hake *Urophycis tenuis*) in various sized patches of simulated eelgrass at Canning's Cove (CC) and Mt. Stamford (MS). Values represent a mean of 9 snorkel surveys of two replicate patches ± 1 SE.

Fig. 6; Proportion of common piscivorous predators (Greenland cod *Gadus ogac*, cunners *Tautogolabrus adspersus* and white hake *Urophycis tenuis*) distributed over a range of artificial eelgrass patch sizes and equivalent areas at natural eelgrass meadows. Expected lines are calculated assuming a linear distribution of fish with area. Actual distributions are plotted with a best-fit quadratic equation to illustrate trends deviating from the expected linear distribution.

Fig. 7; Percent predation of juvenile cod (*Gadus* spp.) tethered in unvegetated areas (0 m^2) and artificial eelgrass patches (0.32, 1.1, 5.5, 11, 22 m^2) at Canning's Cove (CC) and Mt. Stamford (MS) between 1999 and 2000. Values consist of 12-36 tether sets and are staggered ± 0.1 m to avoid overlap

Fig. 1

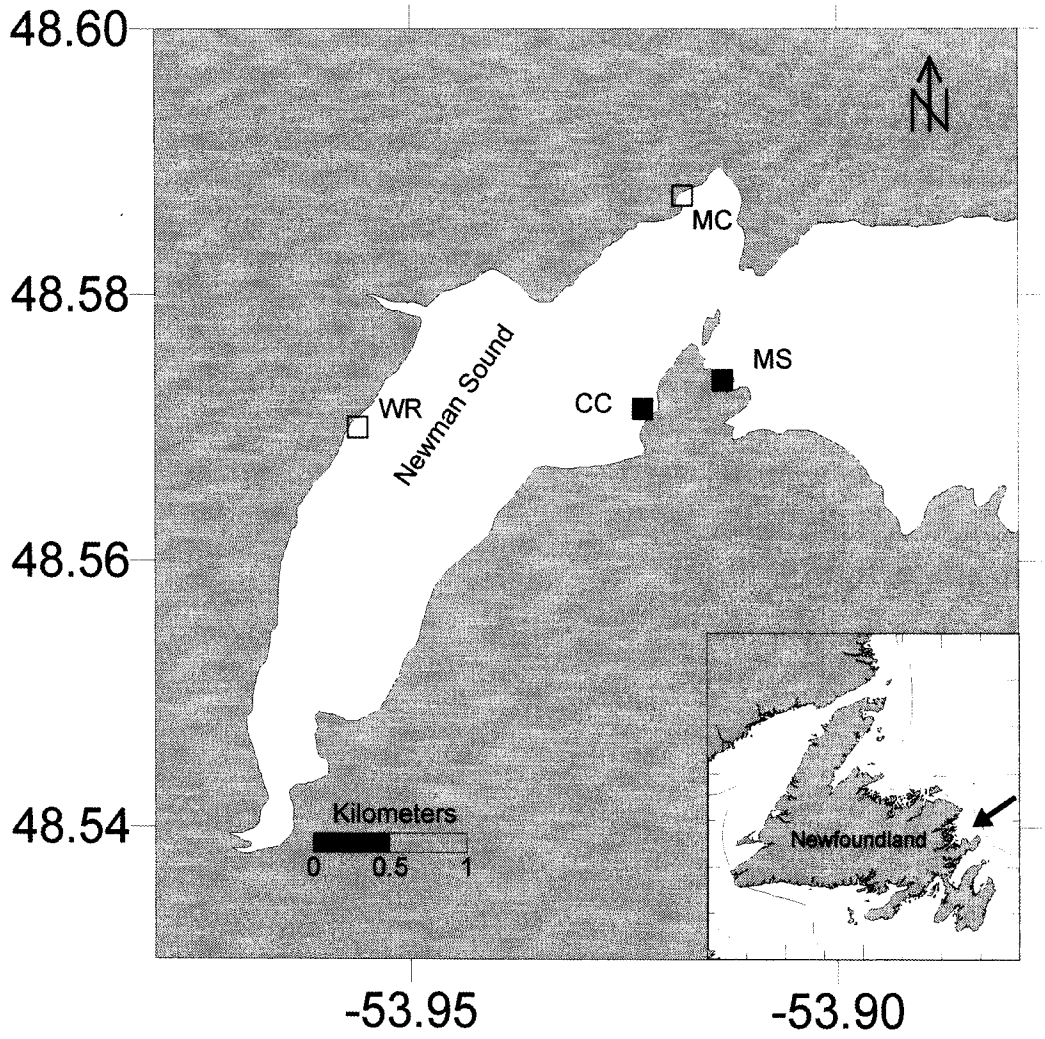
48.60
48.58
48.56
48.54
-53.95
-53.90
N
MC
MS
CC
WR
Newman Sound
Kilometers
0
0.5
1
Newfoundland

Fig. 2

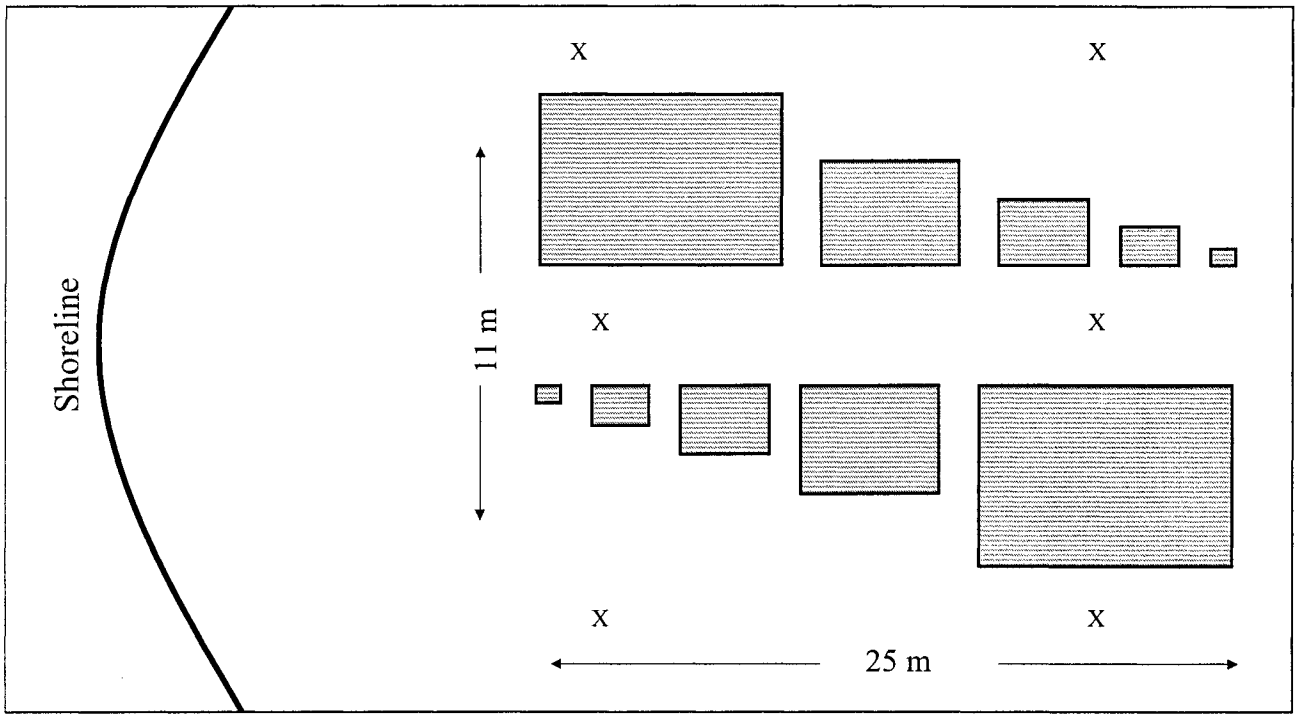

Fig 3:

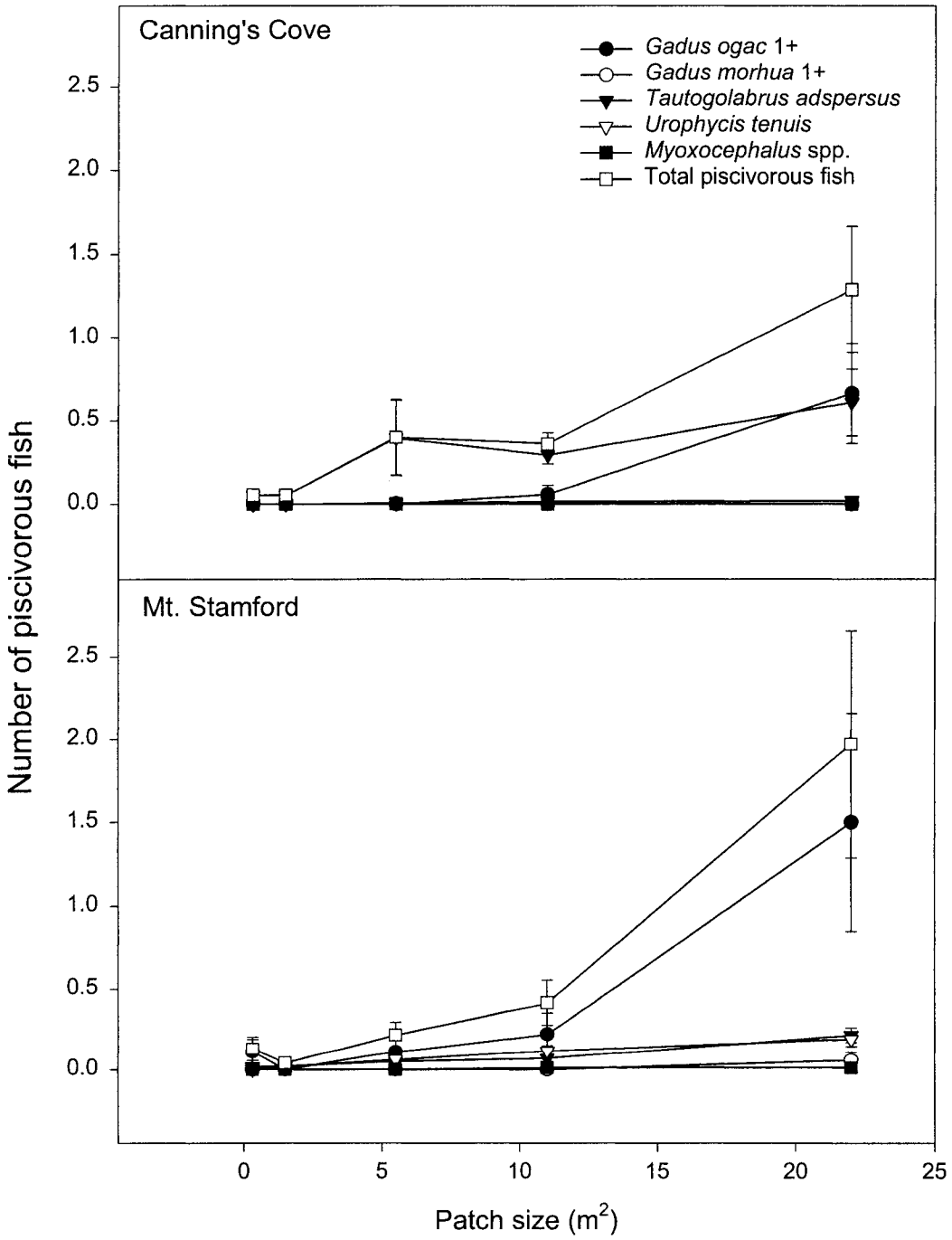
Canning's Cove
Gadus ogac 1+
Gadus morhua 1+
Tautogolabrus adspersus
Urophycis tenuis
Myoxocephalus spp.
Total piscivorous fish
Mt. Stamford
Number of piscivorous fish
Patch size (m2)
0.0
0.5
1.0
1.5
2.0
2.5
0
5
10
15
20
25

Fig 4:

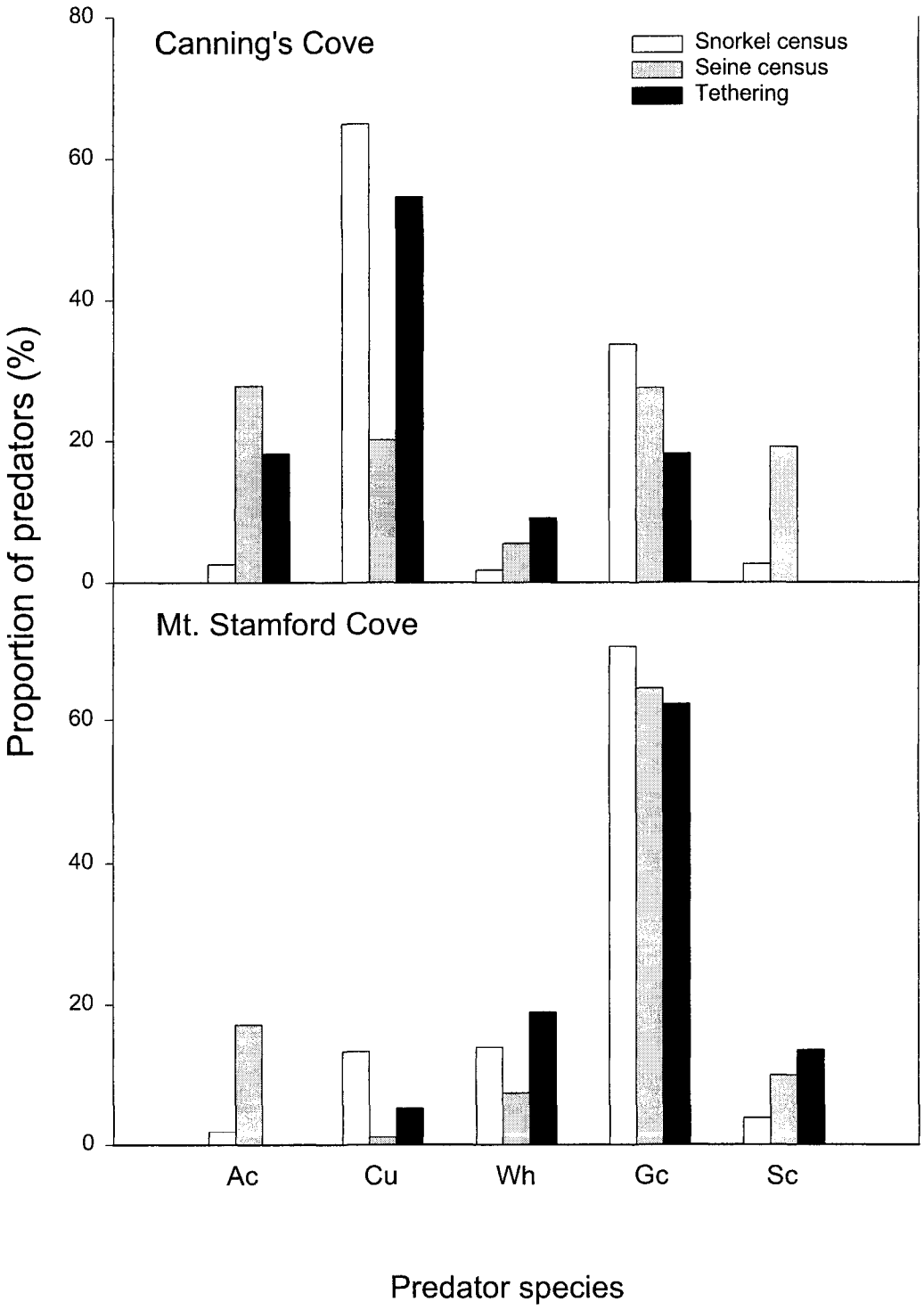
Canning's Cove
Snorkel census
Seine census
Tethering
Mt. Stamford Cove
Proportion of predators (%)
80
60
40
20
0
Ac
Cu
Wh
Gc
Sc
Predator species

Fig 5:

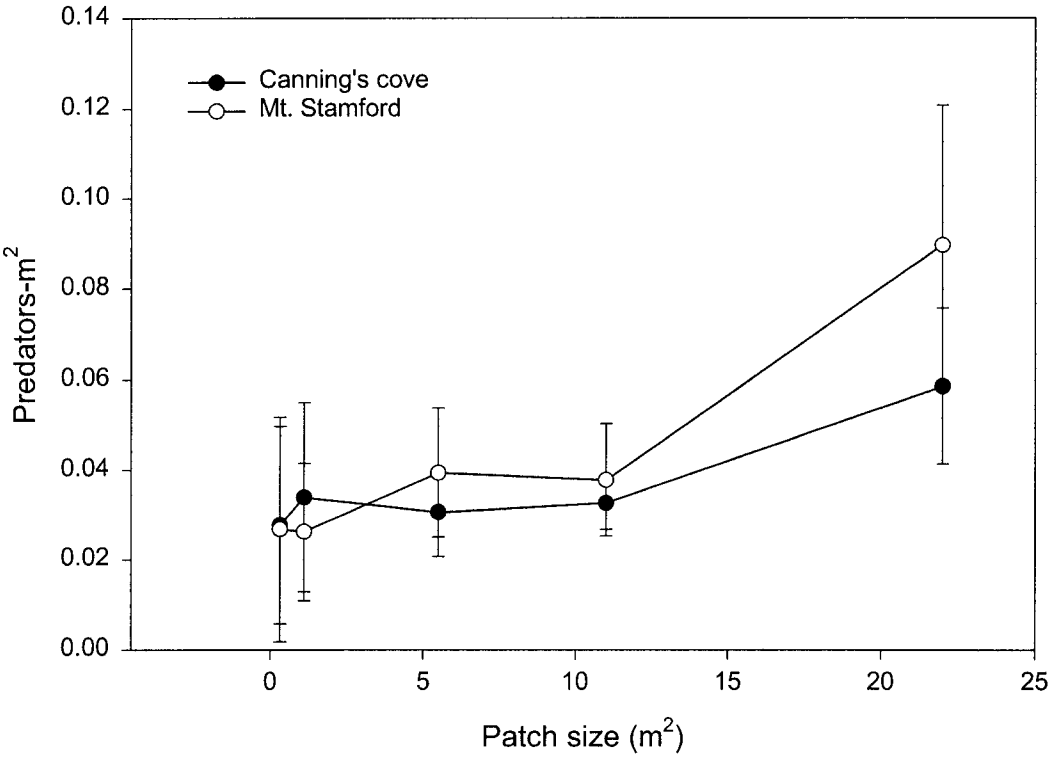
Canning's cove
Mt. Stamford
Predators-m^2
Patch size (m^2)
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
0
5
10
15
20
25

Fig. 6

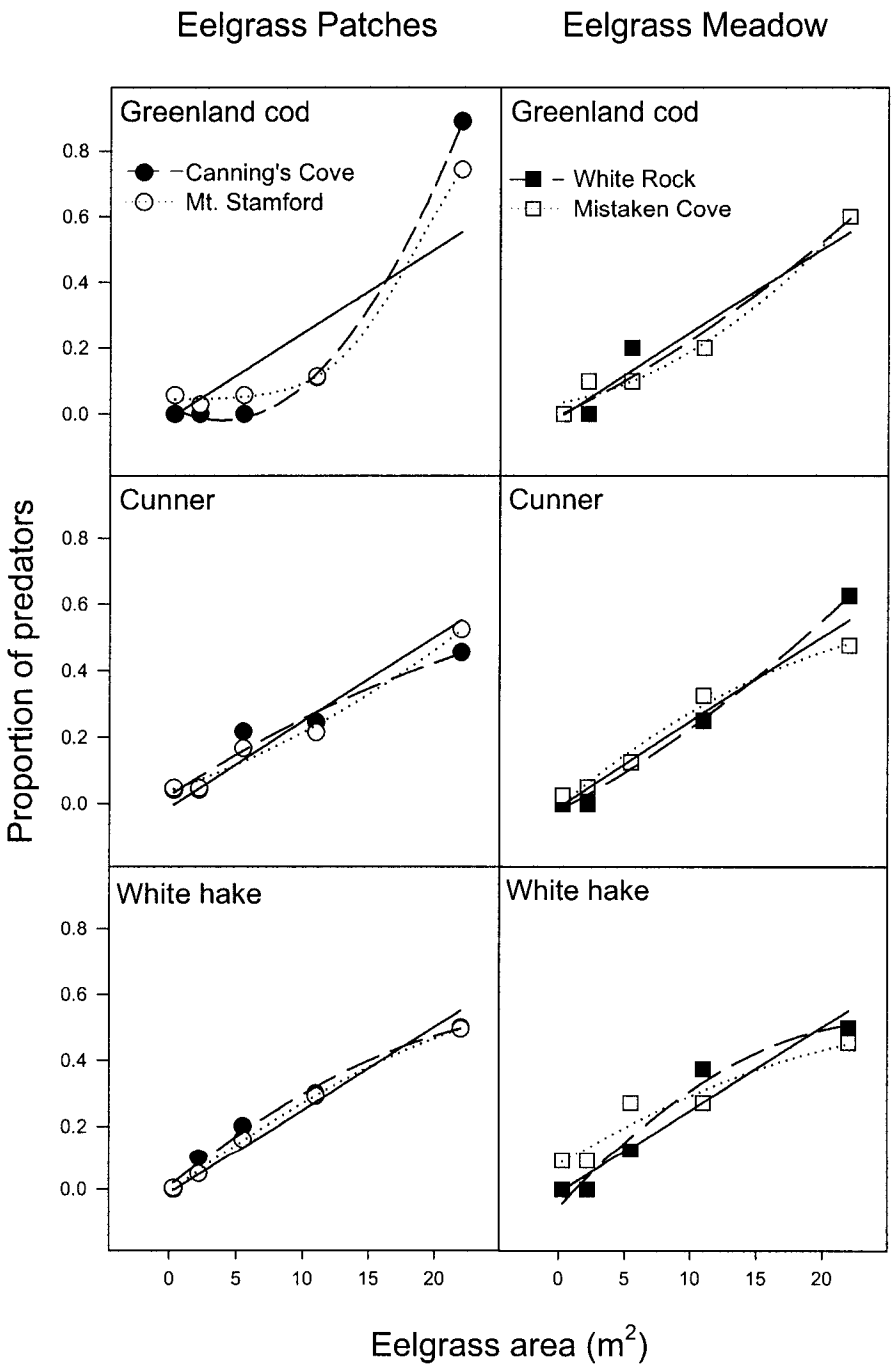
Eelgrass Patches
Eelgrass Meadow
Greenland cod
Canning's Cove
Mt. Stamford
Greenland cod
White Rock
Mistaken Cove
Cunner
Cunner
White hake
White hake
Proportion of predators
Eelgrass area (m2)
0.0
0.2
0.4
0.6
0.8
0
5
10
15
20

Fig 7:

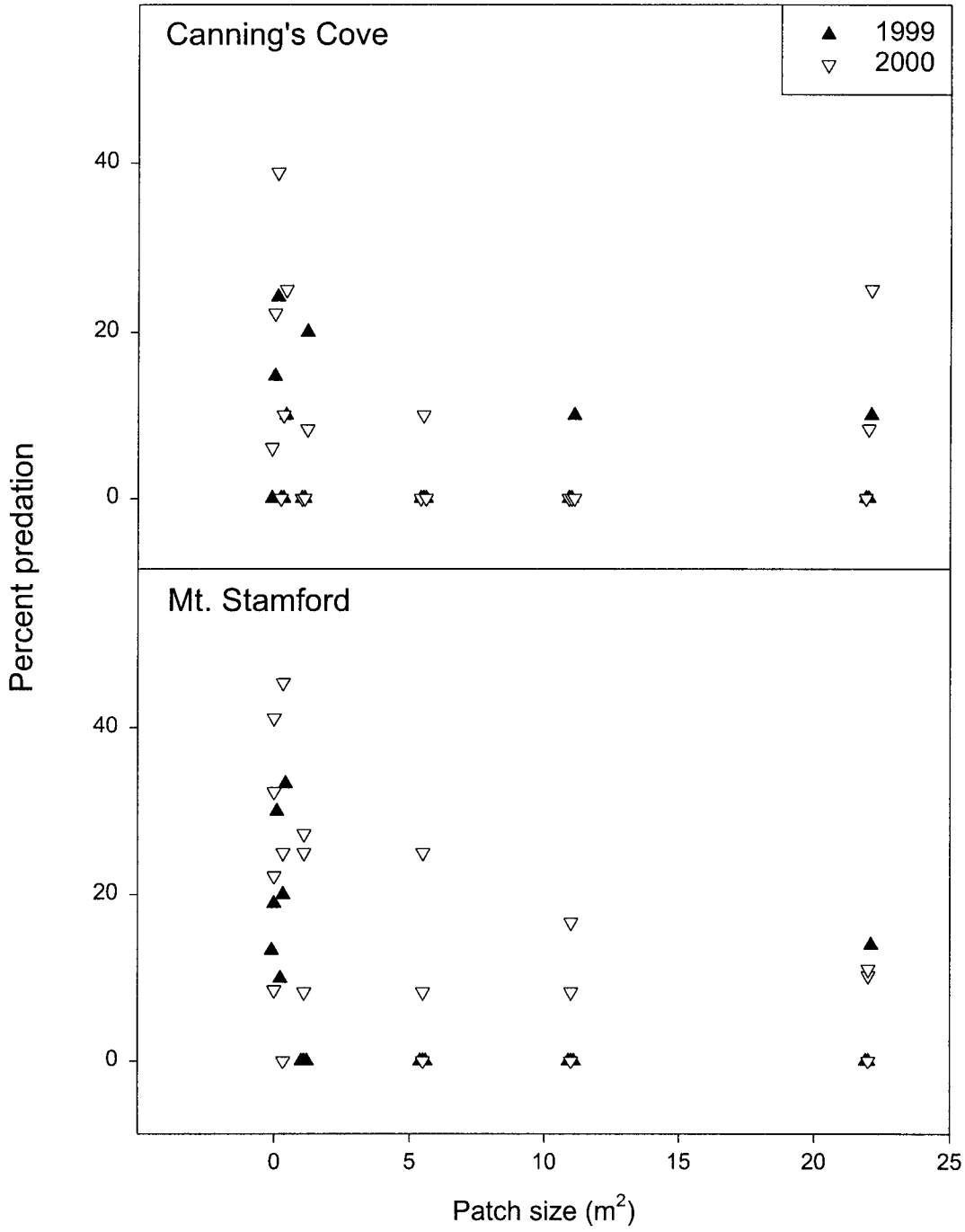
Canning's Cove
1999
2000
Mt. Stamford
Percent predation
40
20
0
0
5
10
15
20
25
Patch size (m²)

Table 1: GENMOD analysis of predation rates of tethered *Gadus* spp. on varying sampling dates and artificial eelgrass patches as a function of year (1999 or 2000) and sampling location (Mt. Stamford-MS or Canning's Cove-CC).

Site	Year	Source of Variation	df	Deviance	Chi-Square	p
MS	1999	Date	2	35.82	1.24	0.5379
		Patch	1	8.06	27.76	<0.0001
		Patch*Date	2	7.34	0.72	0.6990
		Intercept	207	37.06		
	2000	Date	2	30.63	11.98	0.0025
		Patch	1	21.04	9.59	0.0020
		Patch*Date	2	16.20	4.84	0.0890
		Intercept	276	42.61		
CC	1999	Date	2	30.90	5.95	0.0510
		Patch	1	24.08	14.82	0.0090
		Patch*Date	2	9.70	4.38	0.0810
		Intercept	238	36.85		
	2000	Date	2	42.95	15.27	0.0005
		Patch	1	15.51	27.44	<0.0001
		Patch*Date	2	14.37	1.13	0.5681
		Intercept	278	58.22		

CHAPTER 5:

Influence of predators and habitat complexity on behaviour and three-dimensional spatial patterns in age 0 juvenile cod *Gadus morhua*

ABSTRACT:

There is a spatial conflict between prey and their predators yet both often coexist at high densities within the same habitat. It is uncertain how such close proximity is maintained, but it is assumed that these predator-prey conflicts are resolved at scales smaller than the sampling method used to measure the spatial pattern. For fish prey and predators, measuring spatial pattern is further complicated by a fish's ability to alter both its horizontal and vertical position in the water column. I used a novel method of measuring 3-dimensional positions of fish and their behaviour in the laboratory to determine how predators and prey coexist in the same habitat at small scales (<2m). The spatial patterns and behaviour of age 0 juvenile Atlantic cod *Gadus morhua* and two of their known predators, age 3+ cod and short-horn sculpin *Myoxocephalus scorpinus*, were examined in two habitats (i.e., sand and eelgrass). Both habitat and predator type interacted to form unique patterns of space occupation by predators and prey. Spatial overlap between predators and prey was highest in open habitat in the presence of age 3+ cod (a cruising predator) but lowest in the presence of sculpin (an ambush predator) in the same habitat. In eelgrass, spatial conflicts between predators and prey were resolved along the vertical component; age 0 cod remained above eelgrass in the presence of sculpin but used the structure in the presence of an age 3+ cod predator. Anti-predator behaviour (i.e., predator-prey distance, prey cohesion, angle separation and freezing) was

significantly reduced over eelgrass compared to sand, suggesting eelgrass has lower 'inherent risk' than open habitats. However, predation mortality was similar across all treatments. This raises the question why age 0 cod relax their anti-predator behaviour in complex habitats. I suggest that complex habitats also impair the visual cues needed to perform anti-predator behaviour (e.g., schooling) and locate predators. Alternatively, the reduced anti-predator behaviour in complex habitats may reflect the fitness costs (i.e., lost foraging opportunities) of using these behaviours in all environments.

KEY WORDS: Predator-prey dynamics · Spatial pattern · Coherence · Atlantic cod · Video analysis · Habitat use

INTRODUCTION:

The interaction between habitat and predators is thought to be the principal determinant of fish distribution (e.g., Savino and Stein 1989a, b, Helfman 1986). Complex habitats (e.g. macrophytes, boulders, coral etc) reduce predation risk by interfering with the ability of predators to encounter (Hershey 1985, Laurel et al. 2003, Chapter 4) and capture prey (Savino and Stein 1982, Werner et al. 1983). The refuge of complex habitats is particularly important to juvenile fish as it is during the early life-history when predation risk is highest (Sogard 1992). Consequently, structured habitats generally support higher densities of juvenile fish than less structured habitats (e.g, Edgar and Shaw 1995, Mattila et al. 1999; Laurel et al. In press (a), Chapter 2), either by effects of predation directly (i.e. mortality) or indirectly (i.e. habitat selection). While both behaviour and direct mortality contribute to spatial pattern, it is behaviour that is often considered to be most influential in shaping fish distributions (e.g., Werner et al. 1984, Hugie and Dill 1994).

Predator behaviour (e.g. movement and foraging) is also influenced by habitat as well as the distribution of prey. Generally, predators will shift their effort to areas of high prey concentration, and as a result, predator densities, like their prey, are typically higher in complex habitats e.g., macrophytes (Linehan et al.2001; Laurel et al.2003) and submerged trees (Eklov 1995). Although the physical structure of habitat can impair foraging, certain predators are able to forage with similar success between complex and open habitats (Savino and Stein 1982; 1989a). Within certain stem densities, habitat structure can actually facilitate a foraging predator's ability to capture prey (Savino and

Stein 1989b; Eklov and Diehl 1994). We should therefore expect a range of predator-prey spatial patterns among varying habitats.

Video analysis has aided our understanding of how predators and prey resolve their conflicting habitat use objectives because we can simultaneously examine the behaviour of both predator and prey. Coupled with image analysis software, researchers have been able to move beyond categorical description of behaviour (e.g. schooling, on bottom, etc) to quantitative approaches, which permit robust statistical analysis. Aspects of predator-prey dynamics that have been quantified include reaction latency (Domenici and Batty 1994), interindividual distance (e.g., Sogard and Olla 1997), reactive distance (e.g., Higgs and Fuiman 1998), attack distance (e.g., Krause et al.1998b), activity levels (e.g, swim speed; Ryer and Olla 1998) and angle separation (e.g., Masuda and Tsukamoto 1998).

Video analysis has been a useful tool in understanding predator-prey dynamics in fish, but it suffers a number of shortcomings. Fish are not restricted to a single plane and, as a consequence, determining spatial information is problematic. One solution is to ignore the third dimension component, but this generally restricts research to small aquaria studies with limited water depth to rule out the vertical component of distance estimation (e.g., Gregory and Northcote 1993; Clark and Stephenson 1999). A second solution is to use multiple cameras, but analysis from such arrays can be cumbersome (e.g., Boisclair 1992, Hughes and Kelly 1996). Furthermore, multiple camera approaches relying on side-view line-of-sight are not capable of filming through structured habitat (e.g., Hughes and Kelly 1996).

In the present study, I use a novel, single-camera technique to gather 3-dimensional spatial data on age 0 juvenile Atlantic cod (*Gadus morhua*) and two of their known predators, age 3+ Atlantic cod (a cruising predator) and short-horned sculpin *Myoxocephalus scorpinus* (an ambush predator). Juvenile cod associate with highly structured habitats such as eelgrass in coastal Newfoundland (Laurel et al. In press (a), Chapter 2), but will also use unstructured habitat (i.e., sand) in years of high density (Laurel et al. In Press (b), Chapter 3). Field sampling (i.e., beach seines; 880 m^2) indicates that juvenile cod and piscivorous predators co-occur in both eelgrass and sand (Linehan et al. 2001; Laurel et al. 2003), but the spatial dynamics of predators and prey have not been explored at finer scales in these species. Specifically, I examine how, and at what scales, age 0 juvenile cod begin to disassociate with their predators over structured (i.e., eelgrass) and unstructured (i.e., sand) habitats. I then test whether changes in spatial pattern and behaviour between predators and prey correspond with changes in predation risk between habitats.

MATERIALS AND METHODS:

Fish collections:

Approximately eight hundred age 0 Atlantic cod were collected by beach seine from nearshore areas in Trinity Bay, Newfoundland. Eighty predators (40 age Atlantic cod (24.1±4.2 cm; $\bar{x} \pm$ sd), 40 shorthorn sculpin (22.3 ±4.8 cm; $\bar{x} \pm$ sd)) were also collected from beach seines in the same location. Fish were transferred to the laboratory and placed in separate 1 x 1 x 0.5 m holding tanks maintained at ambient temperature (4-

8° C). Age 0 cod were fed a combination of chopped herring and pelleted food every second day and predators were fed *ad libitum* on chopped, frozen herring twice weekly.

Experimental design:

Spatial distribution and behaviour of age 0 juvenile cod and their predators were digitally videotaped over sand and simulated eelgrass in a large flow through tank (2.0 x 1.5 x 0.4 m) maintained at 5-10° C. Digital video was obtained by a camera, fixed with a wide-angle lens, mounted 2.2 m directly above the tank. The field of view and focus of the camera were locked to maintain a clear, perpendicular view of the entire tank and the test fish. An observer in an adjacent room outfitted with a video-screen was able to remotely start and stop trials. Two light stands (1.8m) each fixed with 600-W halogen light sources were placed on opposite sides of the tank. Lamps were angled downward into the tank to illuminate the tank as well as cast a shadow of each fish onto the substrate.

An experimentally naïve predator was introduced to the experimental arena via a trapdoor connected to a holding chamber (0.5 x 1.0 x 0.4 m). Predators were held in chambers and not fed for 24 hrs before use in any trial. Before the onset of a trial, the trapdoor was lifted and the predator was free to swim into the experimental arena. Because the predator was not trained, the time a predator took to enter the arena was variable c. 1-15 min. Once in the arena, predators were allowed to acclimate a further 15 min before the onset of a trial. Immediately after the predator entered the arena, five age 0 juvenile cod (*Gadus morhua*; 7.8 ± 0.14 cm) were transferred from their holding tank and placed into a 2 L transparent starting chamber. Age 0 juveniles were held in the

chamber for 15 min prior to being released into the arena and onset of filming. Following each trial, both predators and prey were collected by dip net and moved to a separate holding tank.

Bottom habitat was rotated between trials to either unvegetated sand or simulated eelgrass. Sand (< 1 mm) was washed and placed into the tank to cover the entire bottom with a 10 cm layer. Mats of simulated eelgrass were placed on top of the sand at a density of 400 blades m^2. Eelgrass was manufactured by attaching green, plastic ribbon (W: 0.8 cm H: 15 cm) to galvanized wire fencing. The wire of the eelgrass mats was buried 1-2 cm in the sand so that only the simulated eelgrass was visible above the sand layer. Total height of blades of eelgrass above the sand varied between 15-16 cm. Ribbon densities fell within the range of eelgrass naturally occurring in coastal Newfoundland areas. Field experiments have demonstrated that similarly constructed eelgrass is selected at settlement (Laurel et al. In press (a), Chapter 2) and serves as a refuge from predators (Laurel et al. 2003, Chapter 4) for age 0 juvenile cod.

Experimental trials consisted of filming age 0 cod (i.e. prey) in the presence of an age 3+ Atlantic cod (28± 3.1 cm SL) or a short-horned sculpin (23± 2.8 cm SL) over each habitat for a 1-hr period (n=10; 40 total trials). An additional set of control trials were filmed of prey, sculpin and age 3+ cod separately over each habitat (n=10; 60 total trials).

Video analysis:

Predator-prey spatial data and behaviour was gathered from video using image analysis software (Matrox Inspector™). Video was analyzed at 3-min intervals during each trial (n=20 reference frames/trial) starting at time 0 min. Because it was difficult to

distinguish the fish against the heterogeneity of the habitat, short 10-s clips of video were examined instead of single video frames. Fish were digitally marked at a reference frame while the video looped to reveal the position of each fish.

Each reference frame was calibrated such that the lower left of the arena image (x, y coordinates) was 0, 0 (cm) and the upper right was 200, 150 cm. Horizontal spatial data was gathered by placing a digital point at the anterior end of each prey and predator in the reference frame. From each digital point, the Cartesian coordinate system of the software outputs a fish position in a 2-dimensional plane (x,y) to the nearest 0.5 centimeter. The vertical component in space (i.e., fish height in the water column) was calculated from the distance of its x,y position to its cast shadow on the substrate. Because the distance of cast shadow is dependent on the position relative to the light source, shadow distances were corrected based on a shadow mapping vector model (see below). In rare instances, the walls of the tank obstructed the shadow cast by the fish. In such cases, I used the vertical position of the same fish just prior to or after being adjacent to the wall. In almost all cases this time was within 3 sec of the reference frame.

In addition to spatial data, I measured the orientation of prey within each reference frame to determine the degree of schooling. Orientation was acquired by drawing a digital line from head to tail of each prey fish in each reference frame (n=5 angles/frame, 100 angles/trial). The software outputs an angle (0-360°) based on the counterclockwise difference between digitally marked fish and a 3 o'clock reference line.

We determined the degree of cohesion between prey groups using an adapted nearest neighbor approach (Clark and Evans 1954). Within a single reference frame, the

interindividual distances between one prey in space (*Ax, Ay, Az*) and a second prey (*Bx, By, Bz*) was calculated using the following equation:

$$1) \qquad Dist_i = \sqrt{(\Delta x^2 + \Delta y^2 + \Delta z^2)}$$

where $\Delta x = Ax - Bx$, $\Delta y = Ay - By$ and $\Delta z = Az - Bz$. The mean distances between fish in each reference frame (n= 10 distances/frame) was then used to give a measure of group cohesion between prey (n=1/frame, 20/trial).

I determined how groups of fish oriented over different habitats (n=10 angle differences/ frame, 200 angle difference/ trial) by examining angle differences between each prey (A_D). The minimal mean (ϖ) of the angle (*Ang*) difference between each fish and its neighbors for each reference frame was calculated using the following equation:

$$2) \qquad A_D = \varpi\left|(Ang_i - Ang_{i+1})\right|$$

where Angle differences were transformed so that $Ang_i - Ang_{i+1} < 180$. If $Ang_i - Ang_{i+1} > 180$, angles were adjusted using the equation:

$$3) \qquad 360 - [Ang_i - Ang_{i+1}].$$

Values of A_D varied depending on the reference fish used to calculate angle differences, so I used the minimal value of five possible values. Lower A_D indicated that fish were

oriented in the same direction whereas A_D suggested that fish were moving in separate directions.

Activity levels of predators and prey were also determined from digital video. Prey activity was noted as either immobile (0) or active (1) at each reference frame in video clips. A proportion of activity based on the five age 0 cod was then assigned to each reference frame (n=20) within each trial. Predator activity was measured over the entire video as the total time spent swimming.

Spatial corrections:

Spatial positions of predators and prey in the tank are only measured in two dimensions (x, y) using image analyses. It is necessary to both determine the third dimension (z) as well as correct for perspective changes between light source and camera. The distance between the measured fish position and its shadow solves for both issues. To begin, it is known that the two measured coordinates of the fish position (x, y) are correct only if the fish is actually sitting on the bottom of the tank i.e., z = 0. Otherwise the fish is at some other point (*F*) along a line between the camera and another point (x y 0) on the bottom of the tank. Let *R* be the point (x y 0). Because shadows are cast in straight lines, given a light source at point *L* and the fish's shadow position *S*, it is known that *F* must lie along a line between L and S. The intersection is the only point which is on both the line $\overline{CR}$ and the line $\overline{LS}$. Thus finding the actual position of the fish is a matter of finding the intersection between $\overline{CR}$ and the light-to-shadow line $\overline{LS}$.

The first computational step involves taking advantage of the fact that any two intersecting lines lie on the same plane. It is known that the light-to-shadow and camera-

to-fish lines both pass through the fish position. Therefore, it is necessary to determine the plane that contains C, L, F and S. Both F and S are unknowns but they are known to be on the same plane as fish positions taken from image analysis (R). The normal for this plane is found by taking the cross product:

$$4) \qquad N = (R - C) \times (L - C)$$

The shadow lies on the ground plane at a point S at the shadow distance (d) from R, the measured fish position on the ground plane. The number of possible values for S is two, as it must lie in the plane with normal N. The projection of N onto the ground plane becomes $N_x N_y N_0$ where N_x, N_y and N_0 are the corresponding vector components of plane N. S is a distance d from R in a direction perpendicular to the projected plane normal. Let M be the normalized perpendicular:

$$5) \qquad M = \frac{(N_x \; N_y \; 0)}{\sqrt{N_x^{\,2} + N_y^{\,2}}}$$

Then S is derived from M:

$$6) \qquad S = R \pm Md$$

The two shadow positions will give different results for the fish position, but the one that places the fish below the ground plane can be eliminated.

It is now possible to compute the position of the fish as the intersection between the camera-to-fish line $\overline{CR}$ and the light-to-shadow line $\overline{LS}$. Calculating the intersection is made simpler by transforming $\overline{LS}$ into an orthonormal coordinate system with an origin at C, x-axis $\overline{CR}$, and z-axis N. The first step in calculating the intersection involves normalizing the axis vectors Z and X:

7) $$Z = N/|N|$$

8) $$X = (R - C)/|\overline{CR}|$$

Using Z and X, it becomes possible to define the rotation transformation T:

9) $$T = \begin{pmatrix} Z \\ Z \times X \\ X \end{pmatrix}$$

Next, the light-to-shadow line ($\overline{SL}$) is parameterized as:

10) $$\overline{SL} = L + Ut$$

where U is the normalized direction from L to S:

11) $$U = (S - L)/|\overline{SL}|$$

The parametric equation is transformed into the coordinate system with origin C and axes T:

12) $L' = T(L - C)$

13) $U' = TU$

The intersection with the x-axis finally becomes:

14) $x = L'_x - L'_y(U'_x / U'_y)$

Lastly, x is used to determine the fish position, which lies along the eye-fish line $\overline{CR}$ at a distance x from the camera. Plugging x into the parametric equation for the eye-fish line gives the final result:

15) $F = C + (R - C)/\overline{CR}x$

or substituting in X gives:

16) $F = C + Xx$

Error in spatial data:

The accuracy of the experimental set-up and corresponding mathematical corrections was determined by estimating positions of plastic poles (1x25 cm) placed in the arena. Digital positions were taken at the tops of the poles throughout the tank and compared against known positions (n=54). Error was low along both the x-axis (1.40 cm± 0.62 SD) and y-axis (1.11 cm ± 0.41 SD). Estimations of height from shadow lengths and corrected x,y coordinates were also similarly accurate (1.36 cm ± 0.66 SD). These methods of finding error do not detect inaccuracies in calibrating the image to a

coordinate set, but rather give an indication of the precision of the experimental apparatus (e.g., light positions, camera accuracy) and the ability of an observer to digitize points from images. Highest error appeared to occur at the corners of the image (i.e., "pincushion effects"), but such distortion is typical of most camera lenses. Hughes and Kelly (1996) discuss methods of correcting radial distortion from camera images prior to image analysis, but the low amount of error from the apparatus did not deem this necessary.

Data analysis:

Horizontal spatial overlap of predators and prey was further examined using a binning technique. Distance between predator and prey in x,y space were first calculated (n=1000) and these values were plotted on an x-y axis so that 0,0 (x,y cm) indicated complete overlap and 150, 200 or -150, -200 indicated maximum avoidance by predators and prey. I then passed an imaginary 15 cm wide transect through the origin of the scatterplot along the y-axis. The frequency of points along the transect were tallied every 15 cm along the entire axis from –150 to +150. Frequency values were collected and plotted against distance from predator to indicate the degree of co-occurrence of predators and prey at increasing scales. Plots were constructed for each habitat-predator combination.

Predation mortality (presence/absence) was examined using a generalized linear model incorporating a binomial error structure (log link; proc GENMOD; SAS Release 6.03). Predator (cod or sculpin) and habitat (eelgrass or sand) were used as explanatory variables.

Prey behaviour (i.e., activity, distance to predator, group cohesiveness, A_D and height) were analyzed with two-way repeated measures ANOVA. Habitat (eelgrass or sand) and predator (sculpin, cod and no predator) formed the between group factors in the model. Time (min) of observation (e.g., 3, 6, 9 ...60) within the trial was examined as a within group factor. Time '0' was dropped from the model since all age 0 cod had a similar starting, clumped position from the initial release from the 2 L container. Data were examined with one-way repeated measures ANOVAs if significant interactions were detected. Paired t-tests were performed post hoc to examine differences between predators in each of the dependent variables. An alpha of 0.01 was used to determine significance for the multiple post hoc tests to account for increased risk of Type I error.

Predator behaviour (i.e., activity and height) was examined using three-way ANOVA with model terms habitat, predator type and presence of prey. A repeated measures design was applied to the model when examining changes in predator height across treatments. Between group factors within the model included habitat (eelgrass or sand), predator (sculpin or cod) and prey (present or absent). Time of observation within the trial was used as the within group factor. Dependent variables were examined with one-way repeated measures ANOVAs if significant interactions between independent variables were discovered. Residuals were examined to determine if they met the assumptions of homogeneity.

RESULTS:

Mortality:

Despite multiple predation attempts (i.e., attacks and chases) observed throughout the experiment, capture success by predators was very low throughout the entire

experiment (11 successful captures total). There was no significant interaction between predator and habitat type on predation mortality ($\chi^2 = 0.29$, p = 0.920, $df = 2$) nor was there any effect of either predator ($\chi^2 = 0.83$, p = 0.811, $df = 1$) or habitat type ($\chi^2 = 0.71$, p = 0.770, $df = 1$).

Predator height:

Differences in predator height in the water column largely reflected the foraging strategies of each predator. Sculpin seldom came off the bottom whereas cod predators generally foraged in mid-water (Fig. 1 and 2). Three-way ANOVA with repeated measures indicated significant interactions between predator and habitat ($F_{1,68}$=21.477, p<0.001) but no interactions between prey and these variables (predator*prey, $F_{1,68}$=0.813, p=0.370; habitat*prey, $F_{1,68}$=0.829, p=0.366; predator*habitat*prey, $F_{1,68}$=0.002, p=0.968). Therefore, I used one-way ANOVAs with repeated measures to examine the effects of habitat and predator independently; 'prey' was dropped from the model. Within habitat analysis indicated a significant effect of predator type in sand (repeated measures one-way ANOVA $F_{1,38}$ =33.756, p<0.001) and eelgrass ($F_{1,38}$ =291.547, p<0.001). In both sand and eelgrass, cod predators maintained a higher position in the water column than sculpin predators. Within-subject analysis indicated these patterns in predator height did not change over time within a trial for sand ($F_{18,684}$=1.029, p=0.424) and eelgrass ($F_{18,684}$=1.219, p=0.132). Within predator analysis also indicated a significant effect of habitat for cod ($F_{1,38}$ =14.501, p<0.001) and sculpin ($F_{1,38}$ =9.356, p<0.004). Within-subject analysis indicated these patterns in predator

height did not change over time within sculpin treatment trials ($F_{18,684}$=1.425, p=0.112) or cod trials ($F_{18,684}$=1.428, p=0.111).

Prey height:

Age 0 cod adjusted their height in the water column in response to predator and habitat type. Generally, age 0 cod were found higher (>8 cm) in the water column in the presence of eelgrass or sculpin compared to cod predators and sand (<5 cm; Fig. 1 and 2). These trends were also statistically significant. Prey height was examined by predator and habitat independently due to significant interactions between these independent variables (2-way repeated measures ANOVA, $F_{2,54}$=18.676, p<0.001). One-way ANOVA with repeated measures indicated that age 0 cod remained closer to the bottom in sand compared to eelgrass treatments in the presence of each predator type (sculpin, $F_{1,17}$=95.087, p<0.001; cod, $F_{1,17}$=26.990, p< 0.001; no predator, $F_{1,17}$=255.798, p<0.001). Prey did not alter their height over the course of a 1-hr trial in any of the treatments (repeated measures ANOVA sculpin, $F_{18,324}$=1.001, p=0.421; cod, $F_{18,324}$=0.640, p=0.891; no predator, $F_{18,324}$=0.778, p=0.782). Significant effects of prey height were also found between habitat types. Prey altered their position in water column differently between predators within sand ($F_{2,27}$=16.513, p<0.001) and eelgrass ($F_{2,27}$=29.387, p<0.001; Fig 3) habitat. Specifically, in sand habitat, prey were closest to the bottom when exposed to a cod predator (x=6.5±2.9) or sculpin predator (x=7.9±1.9), compared with "no predator" (x=13.2±1.1). *Post hoc* tests indicated these differences were significant between sculpin and non-predator treatments (t = 3.643, p=0.001, *df* = 9) but just outside the statistical alpha (0.01) in the cod-no predator comparison (t=2.52, p= 0.042, *df*=9). In eelgrass,

prey were closest to the bottom with cod predators (x=8.9±2.6), followed by sculpin (x=15.4±2.3) and no predator (x=18.3±3.1). *Post hoc* tests indicated these differences were significant in cod-sculpin (t = 4.603, p=0.001, *df* = 9) and cod-no predator comparisons (t = 3.808, p=0.001, *df* = 9). These patterns were consistent across time in each trial as no significant within-subject effects were detected in any comparison (repeated measures ANOVA eelgrass, $F_{18,486}$=1.121, p=0.330; sand, $F_{18,486}$=0.529, p = 0.945).

Predator-prey distance:

Direct contact between predators and prey was rare. When it occurred, contact events were usually the result of a predator attacking a prey, but close contact also occurred when prey inspected predators. Inspections generally involved one or more age 0 cod approaching a predator from behind, which would on occasion result in direct physical contact. This behaviour was infrequent and was entirely restricted to inactive sculpin. Overall, however, age 0 cod generally avoided predators by at least two body lengths (*c.* 15 cm) in the horizontal and vertical plane. Analysis indicated a significant interaction in predator-prey distances between habitat and predator type (2-way repeated measures ANOVA, $F_{2,54}$=25.152, p<0.001). Habitat and predator type were therefore examined independently using one-way ANOVAs with repeated measures. There was a significant effect of habitat on distance between predator and prey for sculpin ($F_{1,17}$=39.418, p<0.001) and for cod ($F_{1,17}$=37.67, p<0.001). However, this was an opposite response. Specifically, prey avoided sculpin more in sand habitat than eelgrass whereas prey avoided cod predators more in eelgrass than sand habitats. This avoidance

pattern was especially evident in the horizontal plane with sculpin predators (Fig 3 and 4). Within-subject analysis indicated no measurable effect of predator-prey distance over time for cod ($F_{18,324}$=1.165, p=0.286) or sculpin ($F_{18,324}$=1.025, p=0.431). Predator-prey distance also varied with predator in sand (1-way repeated measures ANOVA $F_{1,17}$=33.868, p<0.001) but not eelgrass ($F_{1,17}$=1.016, p=0.327). In sand, age 0 cod maintained a greater distance to sculpin than cod (Fig 3 and 5). Within-subject analysis indicated these predator-prey distances did not change throughout the trial for either sand ($F_{18,324}$=1.223, p=0.236) or eelgrass ($F_{18,324}$=1.361, p=0.143) trials.

Predator and prey activity:

Age 0 cod activity changed as a function of habitat (repeated measures 2-way ANOVA $F_{1,54}$=4.665, p = 0.035) and predator (repeated measures 2-way ANOVA $F_{2,54}$=5.893, p = 0.005) without a significant interaction ($F_{2,54}$=1.886, p= 0.162). Age 0 cod activity was lower in the presence of cod predators compared to sculpin and non-predator treatments (p<0.001). Cod predators would routinely approach prey rapidly and cause prey to periodically "freeze" (i.e., remain motionless) either at the substrate or air-water interface. However, "freeze" behaviour was not commonly observed in the presence of eelgrass. In eelgrass, prey would react to approaching predators but would maintain activity following predator encounters. There was a slight tendency for prey activity to diminish through each trial but not significantly so despite the large sample size (repeated measures ANOVA. $F_{18,972}$=1.4, p = 0.079).

Predator activity was analyzed by 3-way ANOVA as a function of habitat, presence of prey and predator type. Overall, predator activity increased in all treatments

in the presence of prey ($F_{1,72}$=27.726, p<0.001). However, significant interactions were found between predator and habitat ($F_{1,72}$=4.220, p=0.044) so these model terms were examined separately by one-way ANOVA. Habitat did not influence the activity of cod predators ($F_{1,38}$=0.652, p=0.424) but sculpin predators reduced activity in the presence of eelgrass ($F_{1,38}$=13.115, p=0.001). Overall, however, cod predators were much more active in both habitats (eelgrass-$F_{1,38}$=4432.112, p<0.001; sand-$F_{1,38}$=1998.313, p<0.001) compared to sculpin (Fig 6).

Group cohesion:

Group cohesion was dynamic in all habitat-predator treatments (Fig 7ab) but an increase in aggregation could be seen in all predator treatments compared with controls (Fig 7cd). Aggregations formed and dispersed as individuals joined and left the group throughout the 1-hr trials. Groups would often be disrupted immediately following a predator attack, but would generally regroup by the next observation period i.e., 3-min later. Group cohesion of age 0 juvenile cod varied with both predator (repeated measures 2-way ANOVA $F_{2,54}$=54.098, p=0.022) and habitat ($F_{1,54}$=18.645, p<0.001) without significant interaction ($F_{2,54}$=0.038, p=0.963). Prey formed more cohesive groups in the presence of sand (40.4 cm±3.2) and cod (43.1cm±2.6) than sculpin (52cm±2.1) and eelgrass (62.1cm±3.1) treatments. Prey groups also became less cohesive through time as indicated by a significant within-subject effect ($F_{18,972}$=6.815,p<0.001). Within treatment changes were confined to the first 20-min of any given trial (Fig 7), during which time prey seemed to become increasingly dispersed.

Angle separation (A_D):

Angle separation (A_D) differed among habitats (repeated measures 2-way ANOVA $F_{2,54}$=7.913, p=0.007) and predators ($F_{2,54}$=74.602,p<0.001) without any significant interaction ($F_{2,54}$=1.401, p=0.255). Lowest A_D values (fish most similarly oriented) were observed among prey in the presence of cod predators 37.5±1.1° (mean±SE) compared to sculpin 42.7±1.7° and no predators 58.0 ±1.8°. Paired t-tests indicated significant differences between all predators (p< 0.01 in all cases). Between habitats, age 0 cod were more randomly oriented in eelgrass 61.4±1.3° than in sand 56.0±1.1°. However, angle separation for all treatments combinations was less than 90° (the value expected if all fish were oriented randomly; Fig 8).

DISCUSSION:

Predator-prey interactions across habitats of varying complexity have been shown to have considerable effects on the behaviour and spatial patterns of fish (Savino and Stein 1982, 1989a, b, Angermeir 1992, Eklov 1995, Linehan et al. 2001, Laurel et al. 2003, Chapter 4). In my study, age 0 cod altered their behaviour in response to changes in habitat and predator type, and similarly, both cod and sculpin predators changed their behaviour in response to the presence of prey species and habitat structure. My study demonstrated an interaction between habitat complexity, predator type and prey, resulting in behaviour and spatial patterns unique to each treatment combination. Some of the changes in spatial pattern were subtle (e.g., <10 cm), and could have been missed using simpler two-dimensional mapping techniques. Other behavioural patterns were more apparent (i.e., schooling and aggregation), and consequently have important bearing on

methods of estimating abundance across habitats. Surprisingly, no differences in age 0 mortality were observed between treatments. These results are discussed in turn.

Predator-prey spatial overlap:

Predators and prey influence each other's distribution and behaviour, making it difficult to consider both in same theoretical framework. Consequently most predator-prey studies are from a single perspective, and can be categorized as foraging studies (predator perspective) or predator risk studies (prey perspective) (see Gregory and Northcote 1993 for exceptions). It has been hypothesized that predator-prey distributions should overlap when the predator response (i.e., mobility) dominates and diverge when the prey response dominates (Sih 1984). In other words, more mobile predators will tend to overlap to a greater extent with prey than less mobile predators. Activity levels reflected these differences in mobility between cod and sculpin predators. Sculpin were actively mobile only 15% of the time throughout trials. In contrast, cod predators were swimming 83% of the time. I observed overlapping spatial distribution in the horizontal component (x,y) of trials over sand; spatial overlap between predators and prey was highest in the presence of the cruising predator but lowest in the presence of sculpin. In eelgrass, spatial conflicts between predators and prey were resolved in the vertical component; age 0 cod remained above eelgrass in the presence of sculpin but used the structure by moving further toward the substrate in the presence of a cod predator.

While many studies have examined spatial overlap of predators and prey (e.g., Sih 1984, Fairweather 1988), my study is novel in its three-dimensional examination of

predator-prey interaction. To my knowledge, no laboratory study on predator-prey behaviour has quantified distribution beyond two dimensions, likely due to the difficulty in acquiring three-dimensional information from two-dimensional images. However, the results clearly show the third-dimensional pattern (height in water column) of habitat use is important in both predator foraging and predator avoidance by prey. These changes in height were often subtle (*c.* 5 cm) between treatments and may have been missed by categorically assigning vertical position as in some studies (e.g, 'top' vs 'bottom'; Savino and Stein 1989b).

The use of three-dimensional spatial analysis was useful in calculating prey group cohesion and predator-prey distances. Focusing on only two dimensions when calculating these distances can potentially overstate proximity because fish can appear clumped (overlapped) in two dimensions when in actuality they are dispersed in three dimensions. In shallow water depths this is of less concern, but overlapping error becomes more problematic as the maximum z-axis (e.g., water depth) approaches the x-axis (e.g., tank width) and y-axis (e.g., tank length) dimension.

In my study, prey were seldom observed among the blades of eelgrass in the absence of the predator. However, they used the eelgrass depending on the presence of a sit-and-wait predator or a cruising predator. Prey moved into the blades of eelgrass in the presence of both predators, but this was pronounced in the presence of a cod predator. Prey may have restricted their use of eelgrass habitat in the presence of sculpin because sculpin waited in ambush amongst the plant stems. Alternatively, prey may have refuged more within eelgrass habitat in the presence of a cod predator if risk was perceived higher among cod predators than sculpin predators.

Predator-prey activity:

Both predators and prey adjusted their behaviour to their environment. Not surprisingly, the activity of both sculpin and age 3+ cod increased in the presence of prey. Heightened activity in response to the presence of prey is typical of most species as they switch from a search to hunting strategy (Gerking 1994). However, only sculpin adjusted their activity level to habitat type. Prey exhibited an increased avoidance response to sculpin in the sand habitat, suggesting sculpin were more visible to age 0 cod in sand than eelgrass. Perhaps as a consequence, sculpin switched from a low-activity ambush strategy in eelgrass to a 'stalking'-type strategy (Gerking 1994) in sand. Cod predators remained equally active in both habitats, swimming ~95% of the time within a trial.

Freezing behaviour by prey was recorded occasionally, usually when fish got separated from the shoal as a result of an attack by the predator. The shoal became dispersed for a short period and occasionally separated individuals would adopt a freezing behaviour either on the substrate or at the air-water interface. Such freezing behaviour is consistent with other observations for other species after they become separated from schools (e.g., Magurran and Pitcher 1987).

On occasion, prey were observed approaching predators but this behaviour was restricted to sculpin in sand habitat. Inspection behaviour has been observed among some prey (Smith 1997) and is suggested to be a means of gathering information on a predator's state and intention (Magurran and Pitcher 1987). The cues fish use to assess risk may be visual (e.g., Murphy and Pitcher 1991) or chemical (e.g., Chivers and Smith 1993). The specific cues that age 0 cod use was beyond the scope of my study.

Schooling behaviour of juvenile cod:

Pitcher (1983) made a distinction between shoaling and schooling behaviour. Both terms describe fish aggregation, but schooling suggests fish are oriented in a similar direction whereas shoaling fish are merely aggregating in a common location. Many studies have explored the fitness benefits resulting from shoaling, primarily from the perspective of predator risk (e.g., Magurran et al. 1992). Fish often school in the presence of a predator or following an attack by a predator (Sogard and Olla 1997, Ryer and Olla 1996, Magurran and Pitcher 1987). Large aggregations of prey can reduce predation risk by either lessening the probability of predator success (e.g., 'confusion effect'; Landeau and Terborgh 1986, Laurel et al. 2001) or diluting risk over a group (e.g., Pitcher and Parrish 1993). Assuming changes in schooling behaviour reflects predator risk, my results suggest that open habitat (i.e., sand) posed a greater risk to age 0 cod than eelgrass. Schooling over open habitats has also been described for other fish species (e.g. Pitcher 1986, Hosn and Downing 1994, Rangeley and Kramer 1998) as well as other taxa (Bertram 1978, Hobson 1978). In my study, I observed an increase in schooling activity in sand, evidenced by decreased angle separation (A_D) and inter prey distance (D_I). Although schooling behaviour is commonly reported in adult cod, my study is the first to provide behavioural evidence of schooling behaviour in age 0 juvenile cod (SL 80 mm). However, such a finding is not atypical. The onset of schooling behaviour can occur at even smaller sizes (e.g., 12mm) in marine fish (Masuda and Tsukamoto 1998, Magurran 1986) and is sometimes more commonly observed in younger than older fish (Sogard and Olla 1997).

It is interesting that juvenile cod also increased schooling behaviour in the presence of cod compared to sculpin. I suggest that increased schooling behaviour of age 0 cod in the presence of predator cod was a consequence of mobility differences between predators. That is, the alternative strategy to schooling (i.e, avoidance) was more difficult for prey when faced with a highly mobile predator. The capability of prey to avoid predators is indicated in the predator-prey distance data of each predator type. The distances maintained between prey and a cod predator was significantly lower than distances maintained between prey and sculpin. The proximity of cod to prey suggests that age 0 cod switch from an avoidance strategy to a schooling strategy when predator mobility is greater.

Fish which are capable of both exhibiting solitary and gregarious behaviour are able to assess and exploit resources in a varying environment (e.g., Ryer and Olla 1995). The costs associated with group living have also been suggested. These costs include increased visual cues to predators (Clifton and Robertson 1993) or increased competition for resources such as food, mates or shelter (Pitcher and Parrish 1993). Researchers have attempted to resolve these conflicts by estimating a theoretically optimal group size. For example, largest group size occurs when the average benefits that individuals accrue from a school just exceed the benefits of a lone fish in the same environment (Giraldeau 1988). Empirical studies demonstrate that group sizes tend to be smaller in structured habitat (Eklov 1995). Presumably group benefits (i.e., foraging and reduction of predator risk) are lower in these habitats than in more open habitats.

Predation mortality:

An interesting result from this study was the similar mortality across all habitat-predator treatments. Although mortality events were infrequent, they were found almost equally between complex (n=5) and open habitats (n=6). This was surprising considering the many laboratory studies demonstrating effects of reduced fish mortality in complex habitats (e.g., Savino and Stein 1989a, b), including studies on juvenile cod (e.g., Gotceitas and Brown 1993, Lindholm et al. 1999). Although other studies have not demonstrated differential mortality between habitats of varying complexity (e.g., Angermeier 1992; Tomcko et al.1984), the number of studies demonstrating refuge benefits of complex habitats has been overwhelming. I am confident the simulated eelgrass in my study provided adequate cover since it closely mimics natural eelgrass and its effectiveness as refuge has been demonstrated in the field (Laurel et al. 2003, Chapter 4). It is possible the contrasting findings in this study are the result of a shorter trial period relative to other studies. Where trials in the present study lasted 1 hr, other predation studies with juvenile cod lasted much longer (2 day, Gotceitas and Brown 1993; 4 days, Fraser et al. 1996; 2 days, Gotceitas et al. 1997; 1.5 days, Lindholm et al. 1999). In certain cases, differential mortality has not emerged at these larger time scales. For example, Fraser et al. (1996) found no differences in mortality of age 0 juvenile cod between habitats of varying complexity. However, latency to capture was significantly higher in complex habitats (Fraser et al. 1996). Over longer time periods, differences in predation-induced mortality begin to emerge, presumably as the costs associated with anti-predator behaviour (e.g., reduced foraging; Lima and Dill 1990) begin to have

physiological consequence. These behavioural costs may not have been manifested in age 0 cod during the 1-hr trial period in my study.

Still, it is interesting that even over the 1 hr trial periods, some predation was occurring, and this predation did not differ between habitats. I am uncertain why anti-predator behaviour (i.e., schooling, distance to predator) was relaxed in eelgrass habitat compared to sand habitat. Presumably age 0 cod could reduce predation risk further by employing anti-predator tactics in complex habitats. I offer two hypotheses as to why age 0 cod relaxed anti-predator behaviour in eelgrass: 1) a 'behavioural impairment' hypothesis where anti-predator behaviour (i.e., schooling and predator avoidance) is constrained by complex habitat or 2) a 'baseline acceptable risk hypothesis' in which predation risk is managed against the potential of lost opportunity.

The 'impairment hypotheses' is supported from several sources. Schooling requires visual cues between group members (e.g., Masuda and Tsukamoto 1998) that could become obstructed in complex habitat such as eelgrass. It has been shown that small, visual feeding fish (5.5-7.0 cm), comparable in size to fish in my study, are less efficient at feeding in eelgrass habitat compared to more open habitats. Similarly, the same visual cues needed to school and forage may also be impaired when tracking the location of predators in complex habitats. Therefore predator avoidance (high predator-prey distance) may be more difficult in eelgrass when the predator is not always visible. Sculpin predators appeared to take advantage of this visual impairment by adopting a sit-and-wait strategy in eelgrass compared to more mobile strategy in sand. Similar behaviour has also been reported in other piscivores. Savino and Stein (1989a) observed largemouth bass shift from searching to ambushing in more complex vegetated habitats.

As a result, bass were able to capture fish equally across all ranges of habitat complexity, yet prey fish still preferred structured habitat to open habitat. Similar switches in foraging behaviour have also reported in perch *Perca fluviatilus* (Eklov and Diehl 1994, Eklov and Persson 1995).

It is also possible that age 0 cod manage their daily activity (i.e., foraging and predator avoidance) around a baseline acceptable risk (*sensu* Walters and Juanes 1993). Although I did not measure trade-offs between anti-predator behaviour and potential missed opportunity (e.g., feeding) in the present experiment, these trade-offs have been quantified in other studies. For example, aggregating fish suffer increased competition when resources are not dispersed (Morgan 1988, Ryer and Olla 1995). "Freezing" and refuging behaviour reduces predator risk but also reduces foraging rates (e.g. Person et al.1997). Therefore, the likelihood of an organism using any anti-predator tactic should be inversely related to 1) predator vulnerability and 2) the potential of missed opportunities (e.g., foraging and mates), while using that tactic. Altering the state of the organism (i.e, hunger or energy budget) can generate a range of outcomes by changing the cost of potential lost opportunities (e.g., Caraco et al.1980; Gotceitas and Godin 1991). These principals form the basis of decision-making in organisms (e.g., μ/g. Werner et al. 1983; Sih 1992). Therefore, similar predation rates could be expected across habitats if the potential of lost opportunities were perceived to be higher in eelgrass than in sand. Measurements of such trade-offs was beyond the scope of my study. Therefore, I speculate on the opportunities for higher growth among different habitats.

CONCLUSION:

Prey managed their predation risk at small spatial scales (meters) by adjusting their behaviour and avoiding predators at smaller scales (centimeters). In open habitats, predator-prey spatial pattern varied largely along the x- and y-axis (i.e. horizontal space). In structured habitat, predator-prey spatial pattern varied along the z-axis i.e. vertical space. Prey also used additional anti-predator behaviour (i.e., schooling, "freezing") in open habitats and in the presence of a cruising predator. Age 0 juvenile cod may use such anti-predator behaviour when alternative tactics such as avoidance and refuging are impossible. Such a strategy resulted in similar predator risk in all predator-habitat treatments, suggesting age 0 cod manage risk around an acceptable baseline rather than a theoretical minimum. It is uncertain why age 0 cod did not minimize risk further in structured habitat. Proximately, such a strategy may stem from an inability of age 0 cod to use anti-predator tactics in all habitats e.g., visual impairment. Ultimately, there may have been fitness costs associated with anti-predator behaviour (e.g., lost opportunity for growth) that were unmeasured in the study. Regardless, the study suggests that small-scale prey behaviour within a habitat may be just as effective in reducing predator risk as a prey's choice of using one habitat over another.

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FIGURE CAPTIONS:

Fig. 1: Predator height off the bottom in sand habitat of shorthorned sculpin *Myoxocephalus scorpius* and age 3+ Atlantic cod *Gadus morhua* in the presence of age 0 juvenile Atlantic cod prey during 1-hr time trial. Each point represents a mean height from ten trials ± 1 SE.

Fig. 2: : Predator height changes over eelgrass habitat of shorthorned sculpin *Myoxocephalus scorpius* and age 3+ Atlantic cod *Gadus morhua* in the presence of age 0 juvenile Atlantic cod prey during 1-hr time trial. The dashed lined represents the height of the eelgrass canopy in the experimental tank. Each point represents a mean height from ten trials ± 1 SE.

Fig. 3: Three-dimensional spatial plots of age 0 juvenile Atlantic cod *Gadus morhua* relative to a predator (shorthorned sculpin *Myoxocephalus scorpius* or an age 3+ Atlantic cod) in sand and eelgrass habitats. Point around the centroid 0,0,0 (i.e., location of the predator) indicate the predator-prey distance (n=968-1000 per plot). The horizontal predator-prey distance is indicated along the x- and y-axis and vertical distance is indicated along the z-axis. Values along the z-axis also indicate the relative vertical position of predators and prey; positive values indicate a predator below the prey whereas negative values indicate a predator above the prey.

Fig. 4: Spatial coherence of predators (Shorthorned sculpin *Myoxocephalus scorpius* or an age 3+ Atlantic cod *Gadus morhua*) and their prey, age 0 juvenile Atlantic cod, in sand and eelgrass habitat. Coherence represents a proportion of prey associated with a predator at a particular distance along the y-axis of spatial data. High values at 0 on the x-axis indicate high overlap between predator and prey at small scales. Data represent horizontal positions (x,y) in space only.

Fig. 5: Distance maintained between predators (shorthorned sculpin *Myoxocephalus scorpius* or an age 3+ Atlantic cod) and their prey, age 0 juvenile Atlantic cod, in sand and eelgrass. Values are plotted over time (min) in an experimental trial. Distances (cm) are derived from three-dimensional spatial data of predators and prey from image analysis. Values represent mean predator-prey distances from ten trials ± 1 SE.

Fig. 6: Activity (time spent swimming) of age 3+ Atlantic cod *Gadus morhua* and shorthorned sculpin *Myoxocephalus scorpius* in sand and eelgrass in the presence or absence of age 0 juvenile Atlantic cod. Values represent mean swim time of predators from ten trials ± 1 SE.

Fig. 7: Group cohesion between five age 0 juvenile Atlantic cod *Gadus morhua* exposed to an age 3+ Atlantic cod predator or shorthorned sculpin *Myoxocephalus scorpius* predator over a) sand and b) eelgrass over a 1-hr time trial. Plots to the right of a) and b) are the relative differences between control and predator treatments in either c) sand or d) eelgrass. Lower values along the y-axis indicate aggregation and high values indicate dispersion. Values represent mean distance of juvenile cod from ten trials ± 1 SE.

Fig. 8: Angle separations (A_D) of age 0 juvenile Atlantic cod *Gadus morhua* exposed to an age 3+ Atlantic cod predator or shorthorned sculpin *Myoxocephalus scorpius* predator over a) sand and b) eelgrass over a 1-hr time trial. Dotted lines represent A_D values if fish were randomly oriented i.e. 90°. Values represent mean A_D of juvenile cod from ten trials ± 1 SE.

Fig. 1

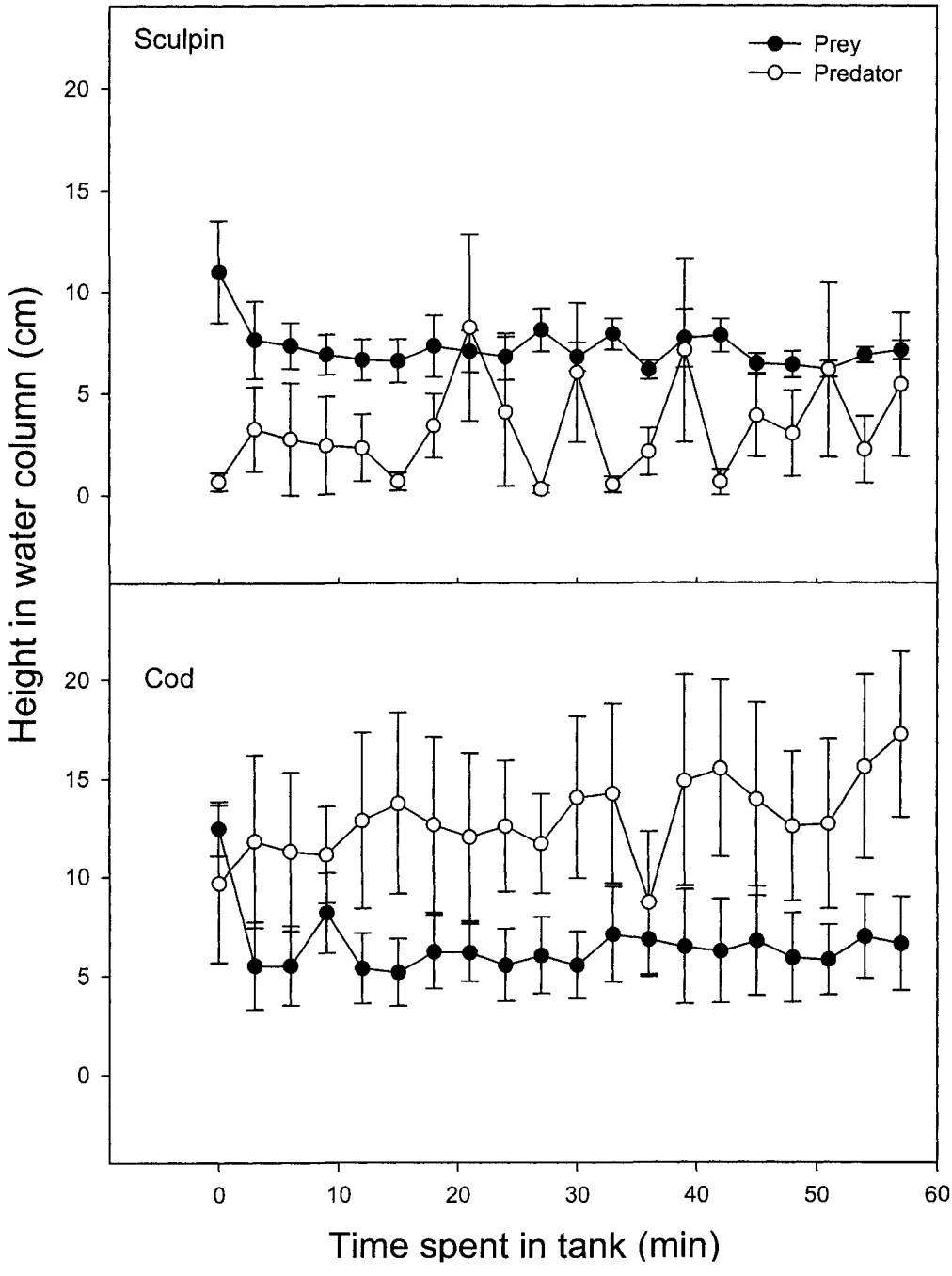

Sculpin
Prey
Predator
Cod
Height in water column (cm)
Time spent in tank (min)
0
5
10
15
20
0
10
20
30
40
50
60

Fig. 2

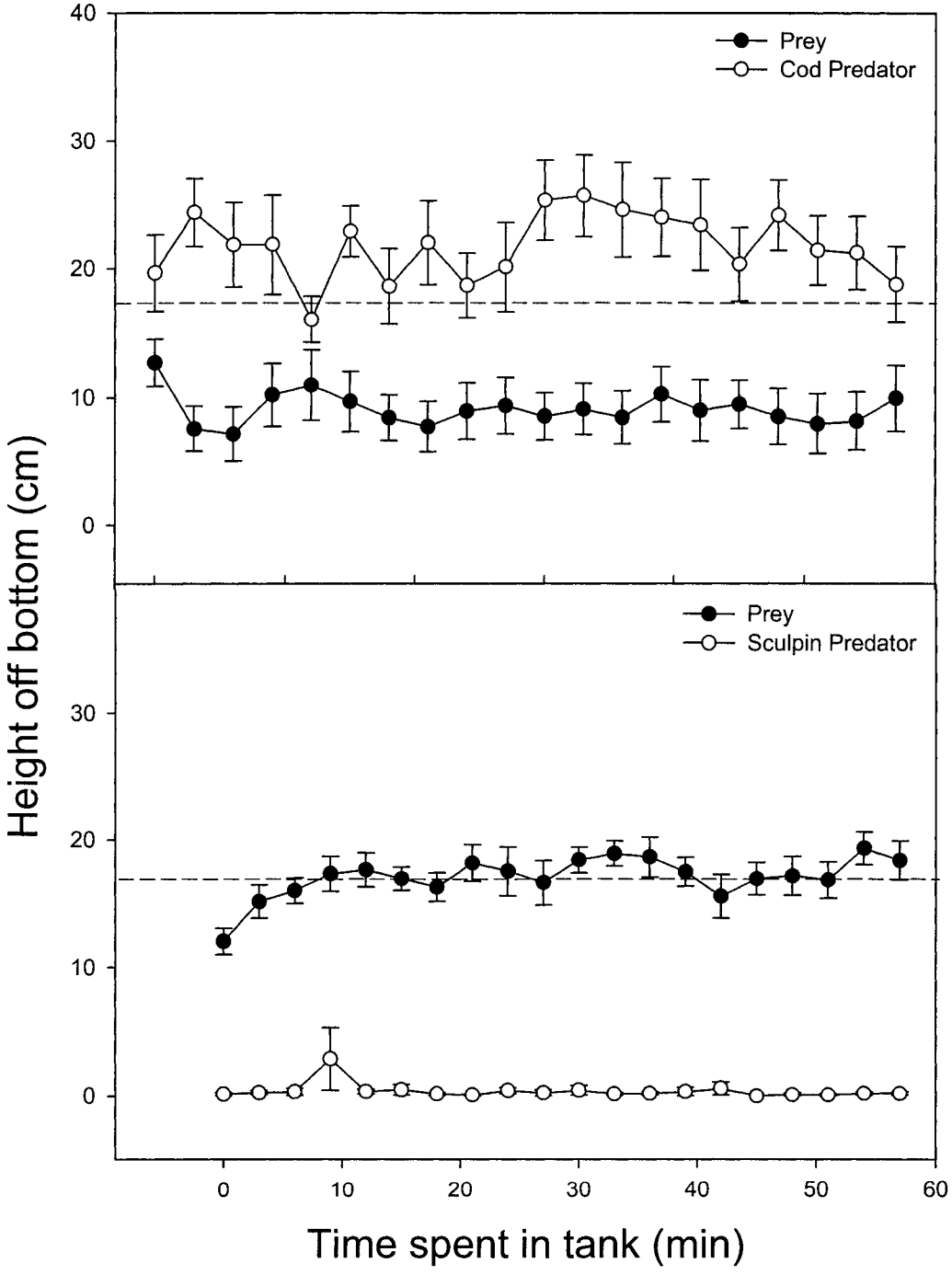

Prey
Cod Predator
Prey
Sculpin Predator
Height off bottom (cm)
Time spent in tank (min)
0
10
20
30
40
50
60

Fig. 3

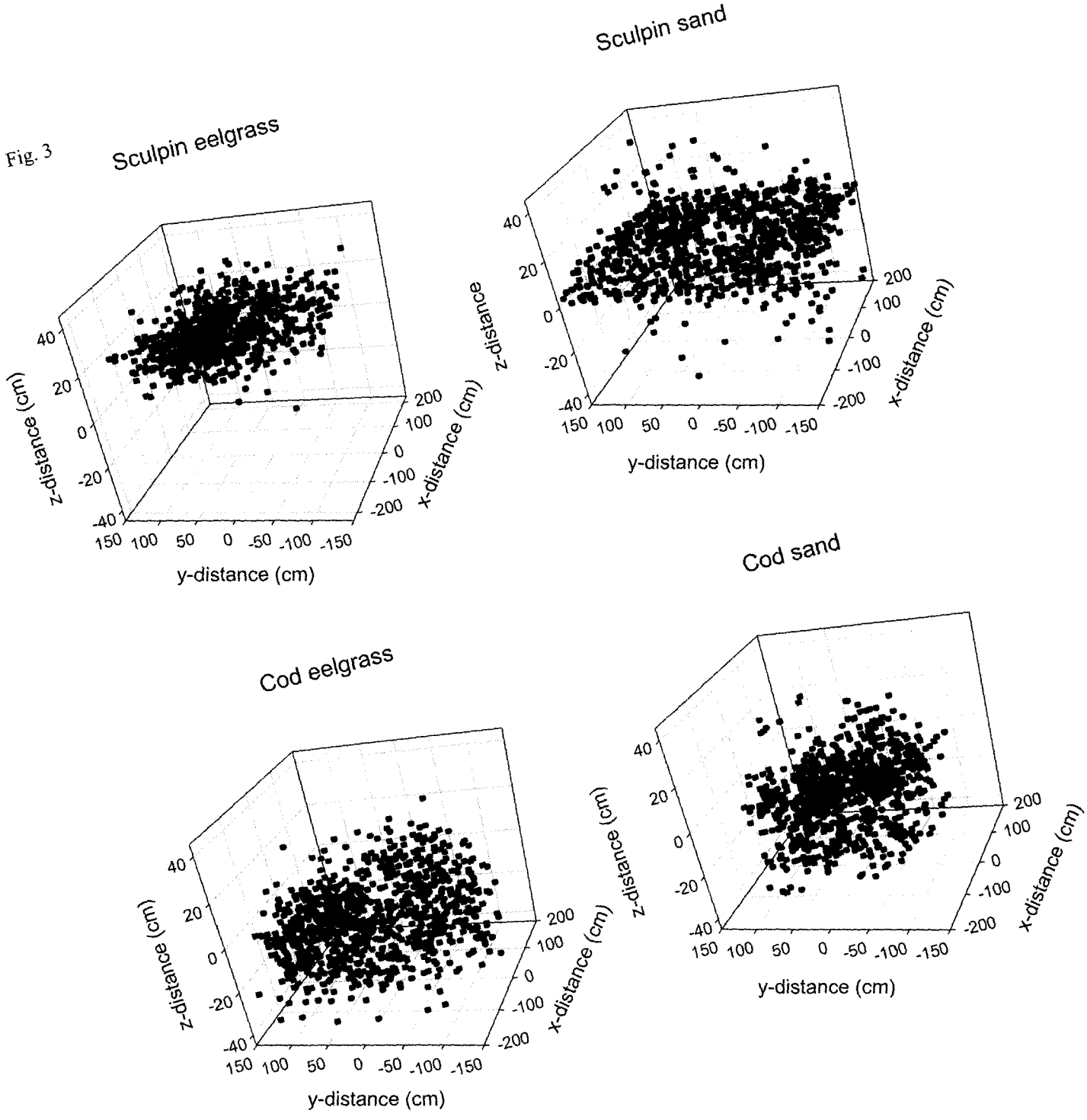

Sculpin eelgrass
z-distance (cm)
40
20
0
-20
-40
150 100 50 0 -50 -100 -150
y-distance (cm)
200
100
0
-100
-200
x-distance (cm)
Sculpin sand
z-distance
40
20
0
-20
-40
150 100 50 0 -50 -100 -150
y-distance (cm)
200
100
0
-100
-200
x-distance (cm)
Cod eelgrass
z-distance (cm)
40
20
0
-20
-40
150 100 50 0 -50 -100 -150
y-distance (cm)
200
100
0
-100
-200
x-distance (cm)
Cod sand
z-distance (cm)
40
20
0
-20
-40
150 100 50 0 -50 -100 -150
y-distance (cm)
200
100
0
-100
-200
x-distance (cm)

Fig. 4

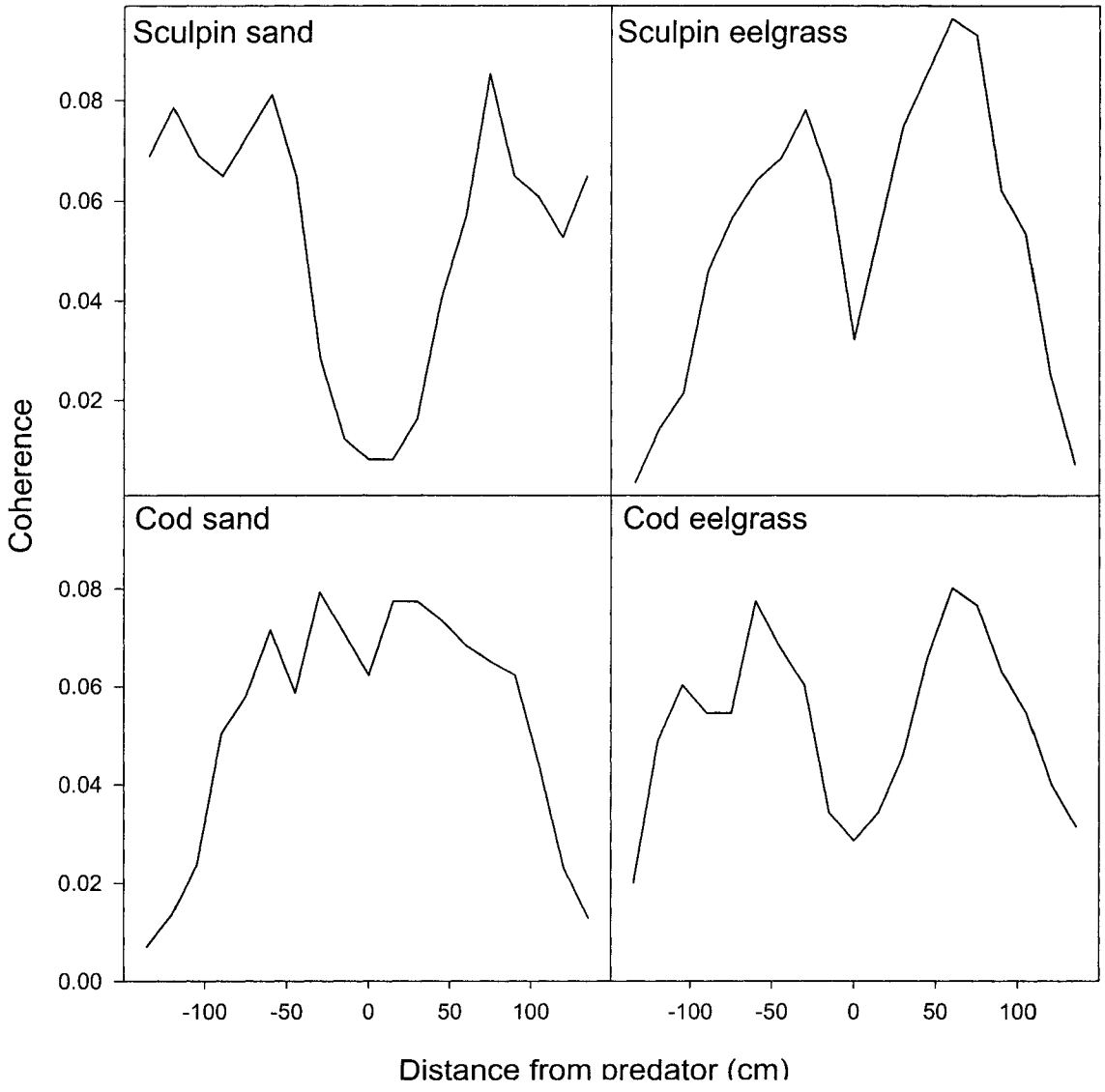

Sculpin sand
Sculpin eelgrass
Cod sand
Cod eelgrass
Coherence
0.00
0.02
0.04
0.06
0.08
-100
-50
0
50
100
Distance from predator (cm)

Fig. 5

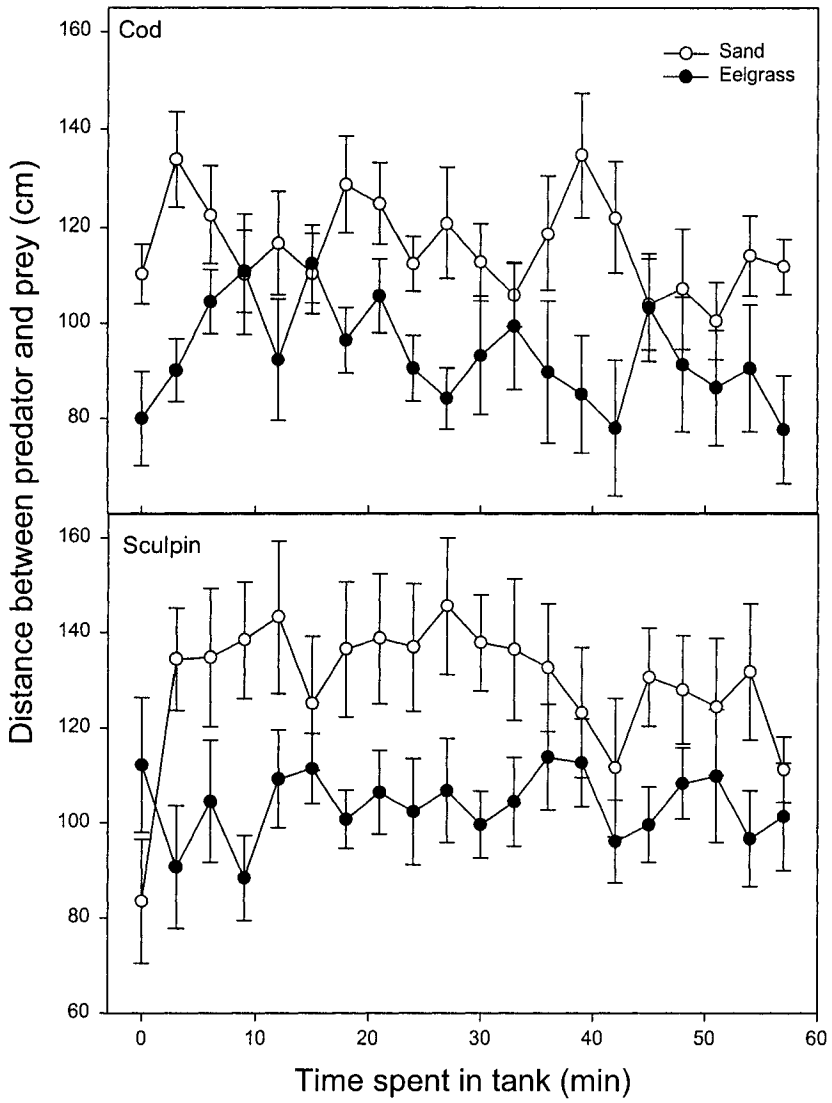

Cod
Sand
Eelgrass
Sculpin
Distance between predator and prey (cm)
Time spent in tank (min)
160
140
120
100
80
60
0
10
20
30
40
50
60

Fig. 6

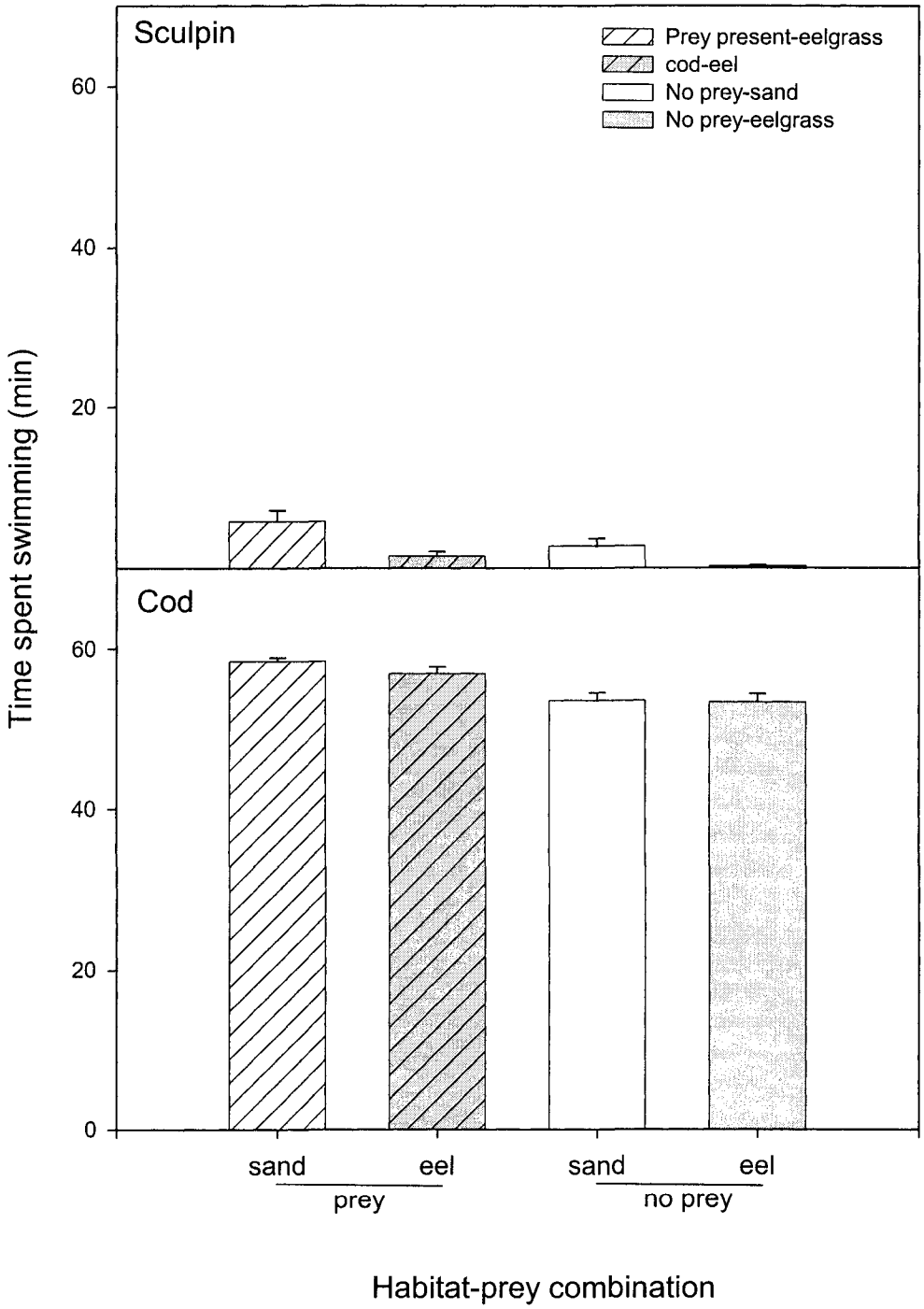

Sculpin
Prey present-eelgrass
cod-eel
No prey-sand
No prey-eelgrass
60
40
20
Cod
60
40
20
0
Time spent swimming (min)
sand
eel
sand
eel
prey
no prey
Habitat-prey combination

Fig. 7

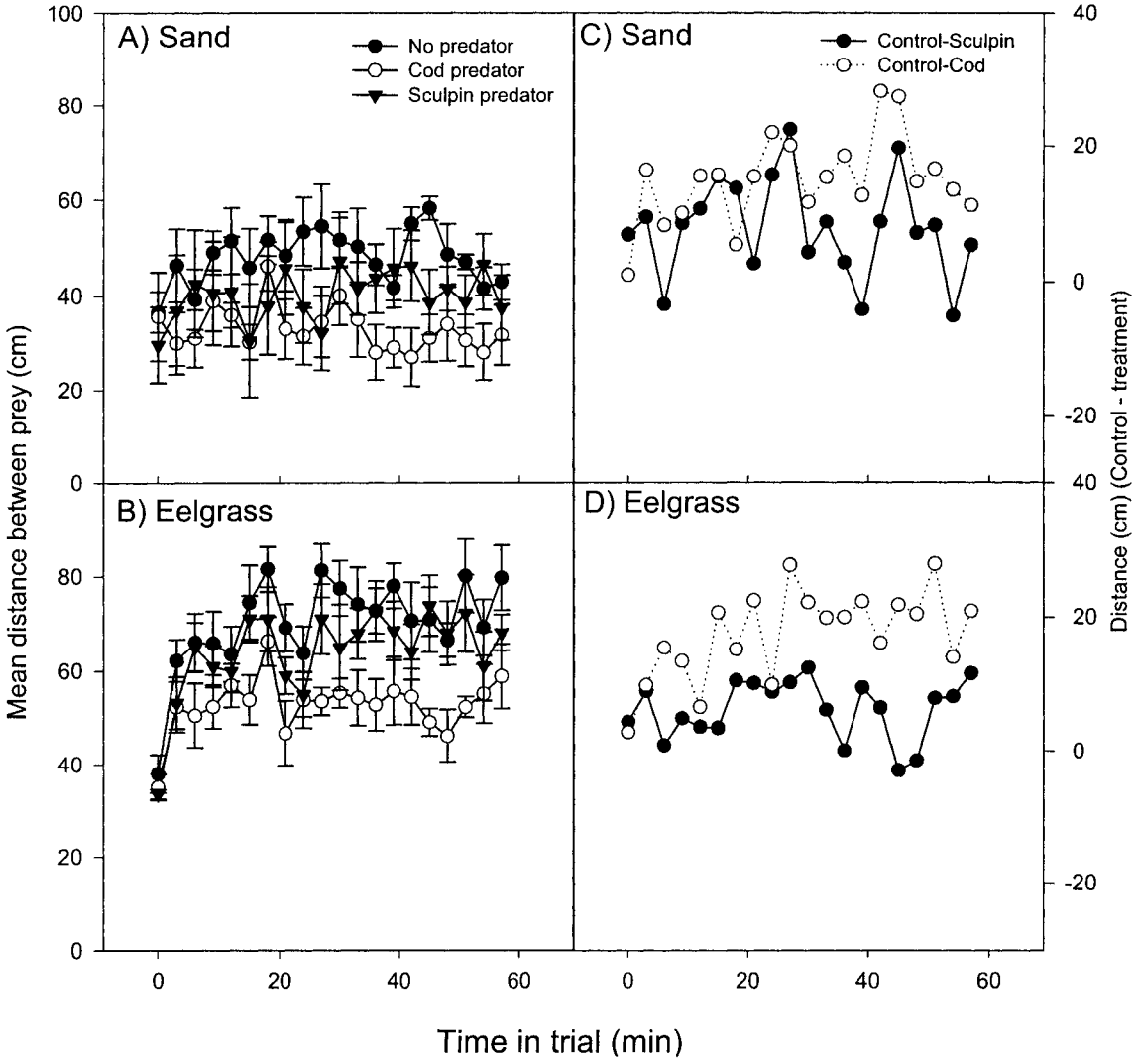
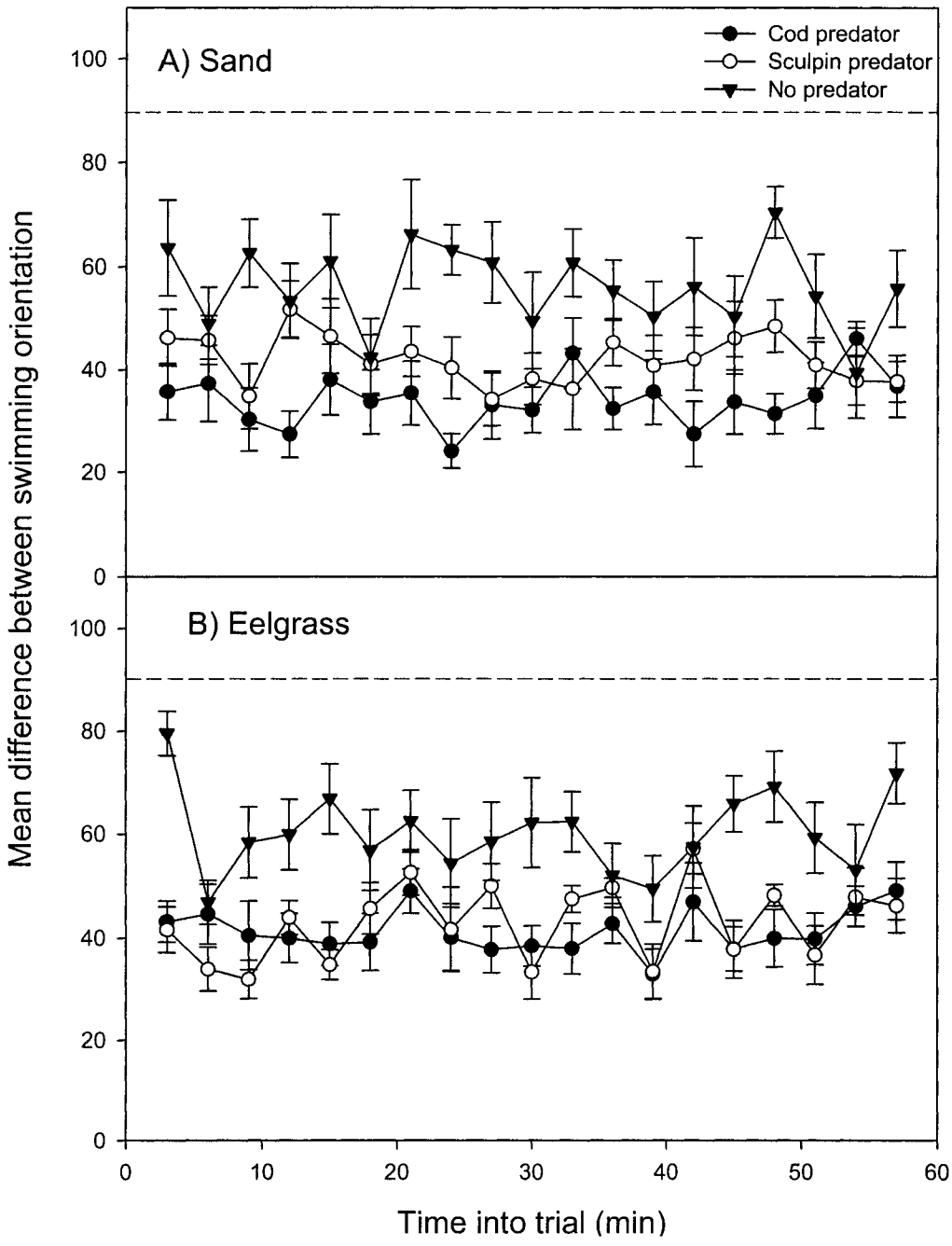

A) Sand
No predator
Cod predator
Sculpin predator
C) Sand
Control-Sculpin
Control-Cod
B) Eelgrass
D) Eelgrass
Mean distance between prey (cm)
Distance (cm) (Control - treatment)
Time in trial (min)
0
20
40
60
80
100
-20

Fig. 8


A) Sand
B) Eelgrass
Cod predator
Sculpin predator
No predator
Mean difference between swimming orientation
Time into trial (min)
0
20
40
60
80
100
0
10
20
30
40
50
60

CHAPTER 6: Thesis Conclusions

Chapter 2 provided the first evidence that age 0 juvenile cod prefer eelgrass habitat at large scales i.e., *c.* 8 km. The experimental design of the study also decoupled eelgrass from other environmental covariates, demonstrating that habitat complexity was correlated with juvenile cod density in the field. Differential habitat use was established during settlement rather than after settlement. The results suggested that settlement might have been delayed until pre-settled forms encounter preferential habitat. Together, these results suggest cod actively influence their distribution at an earlier age than has previously been reported.

Chapter 3 supported two implicit findings of chapter 2: 1) juvenile cod are capable of moving extensively following settlement and 2) juvenile cod aggregate over unvegetated sand in high abundance years. These results indicate juvenile cod are not strongly site-attached, as reported in previous studies. Juvenile cod altered their behaviour to compensate for the use of poor habitat quality when favorable habitat was limiting (i.e., in high-density years). These results have important consequences for estimating abundance and mortality using traditional seining methods. Sampling of juvenile cod should be conducted over multiple habitats and be designed to account for aggregation effects in sand habitat by either sampling large volumes of water or increasing replicate samples. Mortality estimates should be based on mark-recapture since age 0 cod are not site-restricted at scales $<1000m^2$.

Chapter 4 demonstrated that the fitness benefits of eelgrass, as indicated in chapters 2 and 3, were variable. I demonstrated that refuge benefits decreased as a non-linear function of decreasing habitat size patch size. Consequently, the results serve as a

rare example of the effects of habitat fragmentation in aquatic systems. I attribute this relationship to enhanced predation at habitat edges and localized predator distribution. Elevated predator density in large patch sizes resulted in higher predation rates compared to smaller patches. Predator distribution must therefore be considered when examining refuge characteristics of habitat, even at small scales i.e., <22 m^2.

Finally, chapter 5 demonstrated a change of behaviour of juvenile cod and their predators in varying habitats. The three-dimensional spatial analysis of fish positions revealed subtle, dynamic uses of space between predator and prey. Conflicts in predator and prey motives were resolved at very small temporal (1-hr) and spatial ($1.2m^3$) scales. These results prompt a further study in examining distributions of predators and prey at larger scales. For example, chapter 4 results suggest predator density corresponds with increasing predator encounter rates, but it is uncertain how these predators affect prey distribution in and among patches.

It is evident that behaviour, ranging in scales from < 1 m^2 to > 1000 m^2, plays a significant ecological role in shaping distribution among age 0 juvenile cod in the nearshore environment. Behaviour was shown to be responsible for the distributions exhibited by age 0 juvenile cod, not simply differential mortality between habitat types. Consequently, these results have important bearing on conservation measures for Atlantic cod. Specifically, habitat protection measures and the design of marine protected areas (MPAs) both require knowledge of home range, habitat preference, variability of habitat use and fish behaviour (e.g., shoaling). Eelgrass habitat seems like a logical start, but several other considerations should also be taken into consideration. Results from my thesis indicate Atlantic cod are prone to habitat fragmentation through increased edge-

effect predation. At the same time, juvenile cod are not site attached and demonstrate high rates of movement. Therefore, protecting large tracts of intact eelgrass beds may be most effective in juvenile cod conservation than setting aside multiple, smaller beds.